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THE OSTEOLOGY OF SOME AMERICAN PERMIAN VERTEBRATES¹

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ARAEOSCELIS

A few days before the close of the field trip of the University of Chicago paleontological expedition of 1909, Mr. C. L. Baker, a member of the party, discovered in a ravine near the west line of Craddock's Ranch, near Seymour, Texas, a large lot of loose bones lying on the surface. The spot where they lay was within a hundred yards of the road which probably every collector in the Texas Permian region had traveled many times, but had neglected to investigate, because of its unpromising appearance. The bones lay strewn over a considerable area, and included numerous forms, a list of which, so far as they have been determined, I have given in my *American Permian Vertebrates*. About a bushel of bones and fragments of bones were collected from the surface at this time, including some of the forms under discussion. Early the next season Mr. Paul C. Miller extensively excavated the bone-bed with most interesting and valuable results. At one end of the deposit, a little distance from other bones, though on the same level, he discovered a "nest" of small bones. Occurring in the moist clay and isolated, the bones were first disclosed by the plow, which naturally had a rather disastrous effect upon them, small and delicate as they are. As soon as the deposit was recognized, the pieces of clay containing the loose bones, and the various nodules in which others were inclosed were carefully collected. The closely associated bones of the skeletons were more or less cemented together by a hard-clay nodular matrix, which has been removed with difficulty, the more so because much of the preparation had necessarily to be done under a dissecting microscope. Many of the bones protruded freely from the nodules into the soft clay;

¹ *Contribution from the Walker Museum*, Vol. I, No. 8.

others were wholly free; such bones or parts of bones are in most exquisite preservation. Doubtless had the deposit been discovered sooner and the whole mass brought to the laboratory in a large block, carefully bandaged, there would have been many more bones recovered—bones more or less anatomically associated. As it was, notwithstanding the greatest care, many bones and parts of bones were lost, and others were broken, and their restoration has been especially difficult, since the fragments must be adjusted under a microscope, for the greater part.

The whole collection of skeletons covered only a few square feet, and probably represents a dozen individuals in various stages of growth. It is not improbable that the student intent upon the naming of species and genera would have described these specimens as belonging not only to different species but to different genera as well, had he not known the conditions under which they were found. I think, however, that the remains are all conspecific, notwithstanding the different sizes and degrees of growth which they show. Especially do the smaller, long bones show a lack of ossification at the ends. I have figured parts of the skeleton of several of these specimens, but have not attempted to reduce them all to one scale, which could easily have been done, since the various more or less articulated skeletons give the relations between the different parts of the skeletons. I have made no figures, however, of the bones of the young animals, save of the clavicle, which I cannot find among the more adult bones. In case the future "species splitter" reaches the conclusion that I have lumped several allied species under one name, I may say that the larger specimens of humerus and femur, originally figured, may be considered as the type of both species and genus.

One can only conjecture the reason why so many skeletons of animals of one species in various stages of growth should have been fossilized so closely together. Possibly a group of hibernating animals were suddenly overwhelmed and drowned, or suffocated and afterward covered by water.

I may add, that in the hope of acquiring material for the more complete elucidation of the form, and baffled at first in the interpretation of the skull, I have delayed the full description until

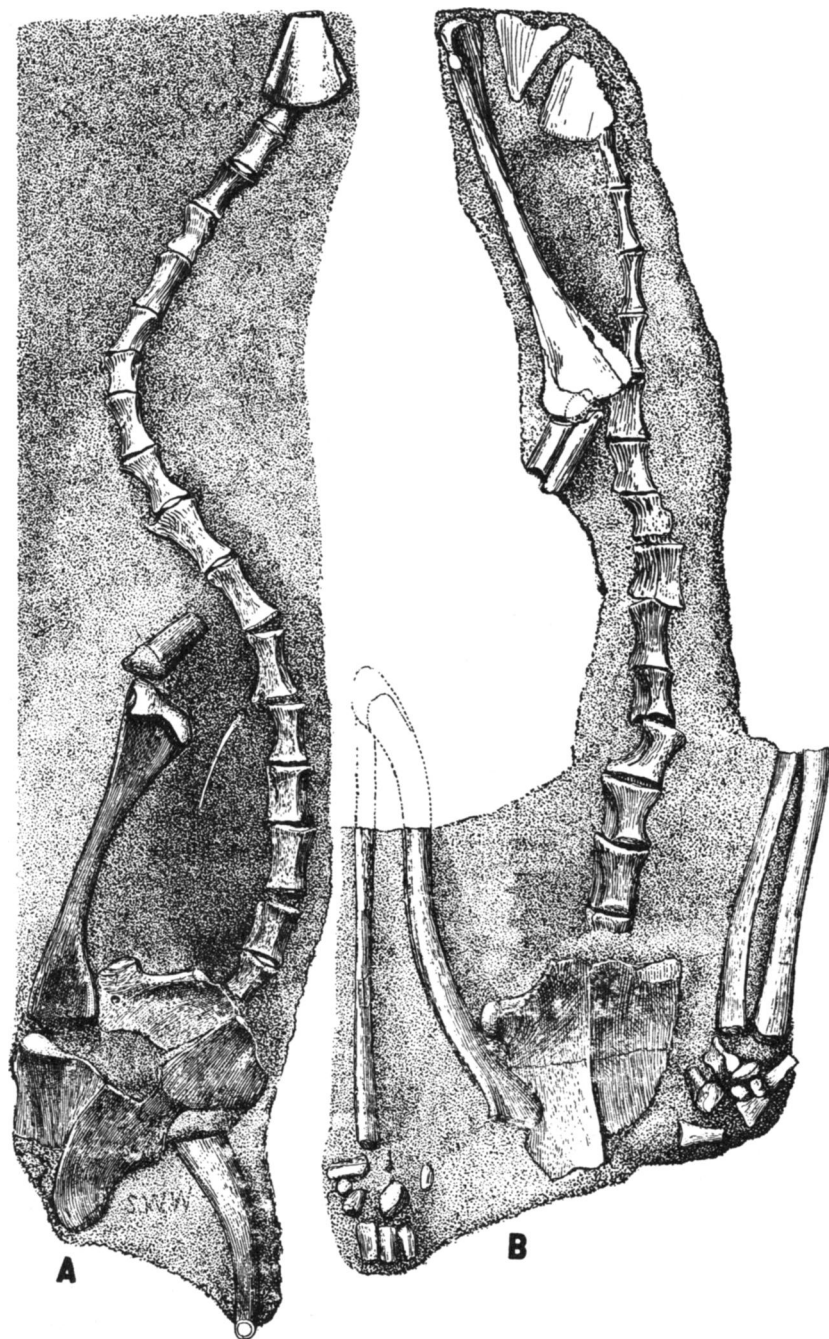


FIG. 1.—*Araeoscelis gracilis* Williston: *A*, part of nearly adult skeleton, as preserved in matrix; *B*, part of adult skeleton, as preserved in matrix. Natural size.

further excavation of the original deposit could be made. Unfortunately, explorations the past year have brought to light only a few more bones, including, however, the skull which has served as the key to the solution of its structure. This delay is the more to be regretted as it has caused Dr. Broom to misinterpret the genus and redescribe it under another name.¹

SKULL

The material studied consists of seven skulls, none complete. They are all more or less distorted, with the different elements more or less separated, and in some misplaced and broken. They also differ in size; two preserved in blocks of matrix in association with cervical vertebrae are of adults; the loose ones are all more or less immature, though none is of a quite young animal.

The first specimen studied, at the time I gave the preliminary description of the genus, had the right temporal region exposed, showing conspicuously what seemed to be the smooth border of an entirely open temporal region. Within the depression, however, there is a large flat bone, and the fragment of another, which seemed to be misplaced elements that had been crowded into the cavity. On the opposite side the same free border was visible with the inclosed space filled more or less by matrix. It was because of this apparent structure that I stated in my preliminary description of the genus that "almost certainly there is a large temporal vacuity" and that "nothing definite can be said about *Araeoscelis* till the skulls have been cleaned and studied, and possibly not even then, save the presence of a temporal vacuity."

Unfortunately for my first belief, when the matrix was removed from the left temporal region of the above-mentioned skull it too was found to have a broad expanse of bone at its bottom, filling out nearly the whole space, definitely proving that the bone of the opposite side belonged where it was found. Nevertheless, distinct evidence of a free border above, and the whole structure of the skeleton so definitely uncotylosaurian, made it difficult for me to

¹ *Araeoscelis gracilis* Williston, *Jour. Geol.*, XVIII (1910), 518; *American Permian Vertebrates* (1911), p. 6; *Jour. Geol.* (1913), p. 743; *Science*, November 9, 1913; Huene, *Morph. Jahrb.*, 1912 (not *Araeoscelis* Schultz, 1911); *Ophiodeirus casei* Broom, *Bull. Amer. Mus. Nat. Hist.* (1913).

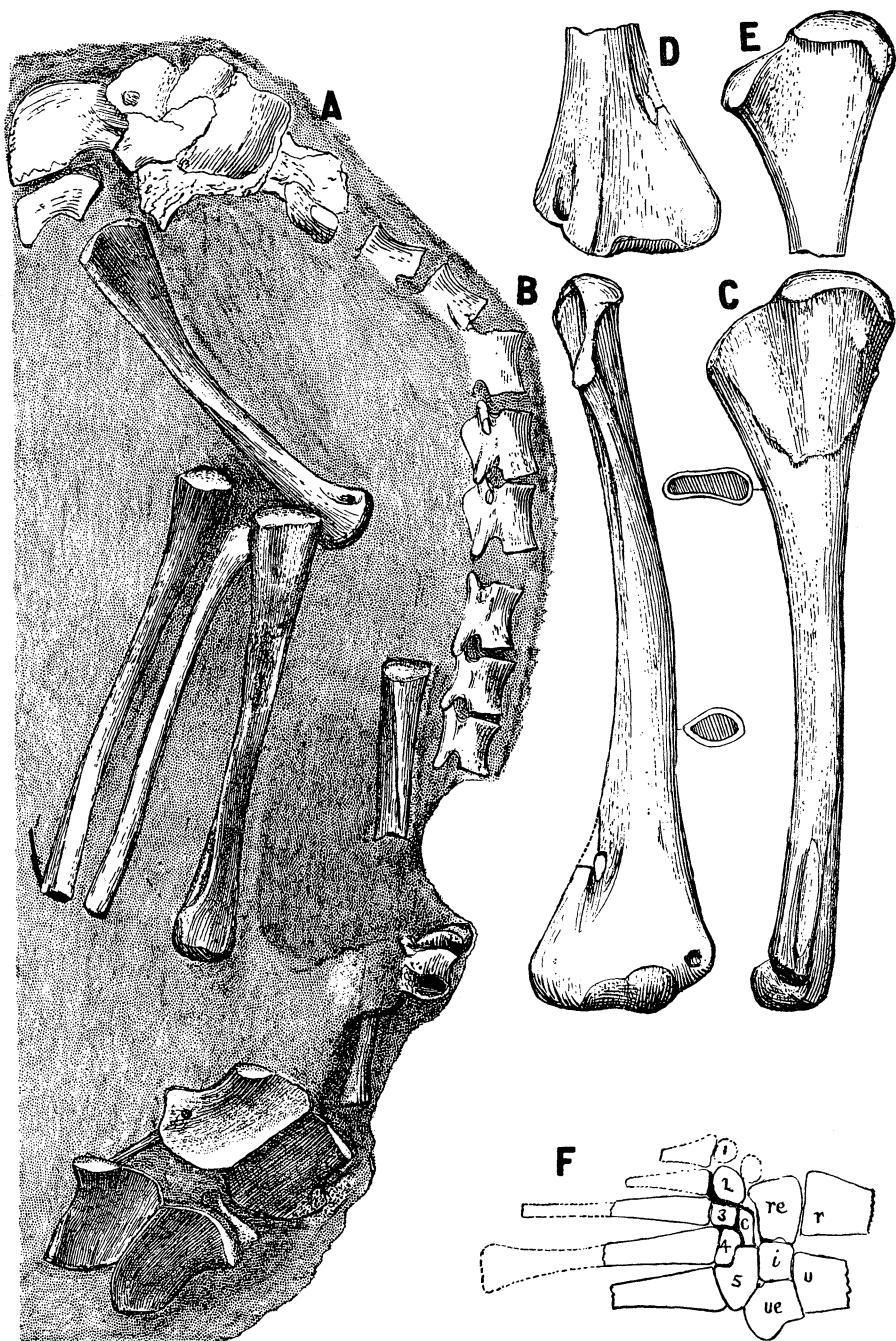


FIG. 2.—*Araeoscelis gracilis*: *A*, part of young skeleton, as preserved in matrix; *B*, left humerus, adult, ventral side; *C*, the same, radial side; *D*, distal end of another left humerus, ventral side; *E*, proximal end of smaller humerus, ulnar side; *F*, part of left front foot. All except *A* enlarged one-half.

believe that the temporal region was closed in. I spent many hours in the endeavor to reach an understanding of the temporal structure, which appeared to be so inconsistent with that of the remainder of the skeleton. That there was only an upper temporal vacuity did not at this time occur to me, since we know of no other paleozoic reptile having such a structure. I had almost despaired of the solution of the riddle when an additional skull was found which shows on the left side the temporal region in an almost perfect condition. With this specimen as a key, the structure of the skull was readily and completely unlocked.

The drawings of the skull herewith given (Fig. 3, *A*, *B*) are composites derived from all the different specimens, though chiefly based on one of about two-thirds adult size. Nearly every character shown or described has been corroborated by several specimens; in the palate only, less corroborative material is available.

In only one specimen is there anything of the premaxillae preserved. In the reconstruction of the general form of the skull I believe that the figures are tolerably accurate, though I cannot be sure that the skull may not have been a little wider or narrower or higher than I have shown it. It is difficult to make exact measurements of such small bones. The preparation of the specimens has required very patient work with a fine needle under a dissecting microscope, for the most part, but the bones, when carefully prepared, come out clean and smooth.

The *parietals* are longer than broad. In one excellent specimen found later, the distinguishing suture in front is clearly shown. The parietal foramen is large, as shown in three skulls; it is situated toward the front part of the parietals, just a little behind the posterior margins of the orbits. Posteriorly, the parietals are produced into an acute angle in the middle, projecting slightly over the supraoccipitals. I can find in no specimen the slightest indication of a distinct dermosupraoccipital, on the upper surface of the skull at least. On the posterior outer angle each parietal is produced into a slender process, as in lizards. In two specimens, the articulating tabulare was cleanly removed, showing a striated sutural surface near the angle. The arch thus formed, of parietal

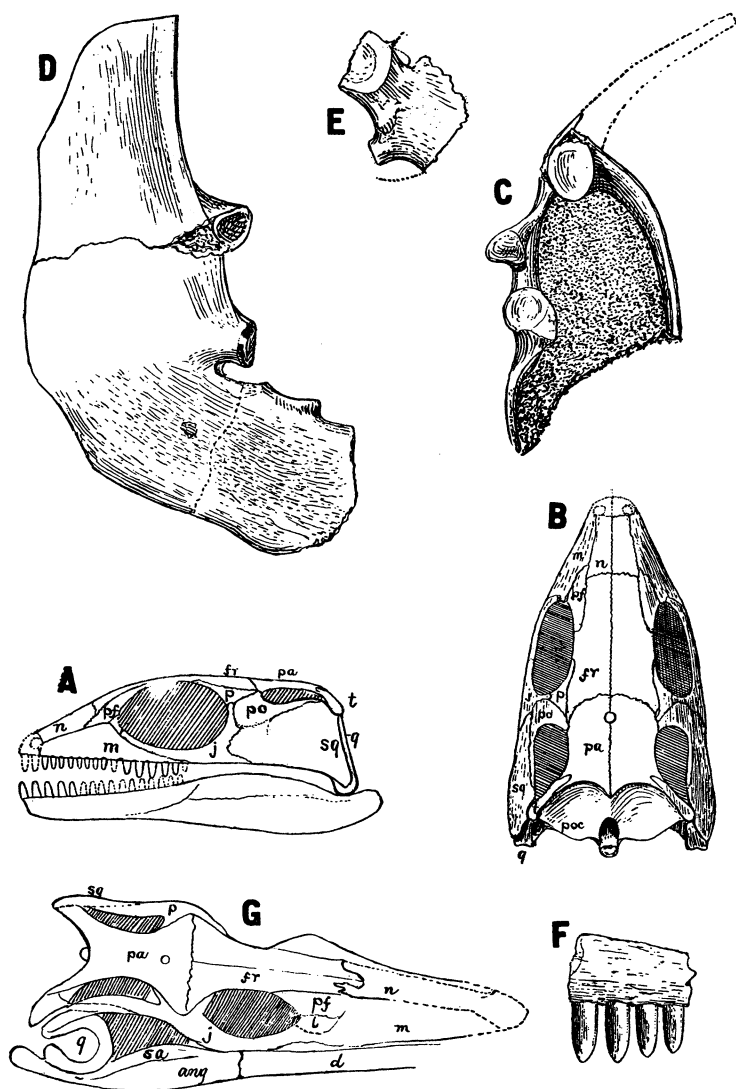


FIG. 3.—*Araeoscelis gracilis*: *A*, skull, about adult size, from the side; *B*, the same, dorsal side; *m*, maxilla; *n*, nasal; *pf*, prefrontal; *pa*, parietal; *poc*, paroccipital; *t*, tabulare; *sq*, squamosal; *q*, quadrate; *po*, postorbital; *p*, postfrontal, *j*, jugal; *C*, left scapulacoracoid, from behind, as preserved in matrix, enlarged one-half; *D*, the same, from the side, the upper end extended in same plane; *E*, part of another scapula; *F*, first four maxillary teeth, much enlarged; *G*, *Opetiosaurus* Kramberger, skull, from above.

and tabulare, is slender throughout, slightly dilated at its extremity, and is directed outward and backward at an angle of about 45 degrees with the long axis of the skull; it is gently curved downward at its extremity to articulate with the squamosal, quadrate, and paroccipital. There can be no doubt of the separation of the element forming the chief part of the arch; I identify it as the *tabulare*. I think that my reasons for so doing are valid. The tabulare in the early reptiles and amphibians is always associated with the outer end of the paroccipital. The only other element that could possibly be in this position is the so-called supratemporal or suprasquamosal. That the present bone is the supratemporal of contemporary authors is, I think, very improbable. This bone is never known to be in relation with the paroccipital and quadrate, relations that the tabulare invariably has; it always articulates with the postfrontal or postorbital when present. I think that doubt of its identity may be dismissed here; it is indisputably the tabulare or "epiotic."

It is now nearly ten years since I wrote the following:

I prefer to call the bone articulating with the postorbital [in the lizards] the squamosal, the bone which in other reptiles articulates with the postorbital behind. Of course if this is the real squamosal, the posterior element cannot be the squamosal. . . . The inner part of the so-called squamosal in the mosasaurs [the posterior bone of the arch] corresponds quite well with the outer part of the paroccipital or opisthotic element, which was not found by Parker in the lizard embryo. Referring now to the figures it will be seen that the outer part corresponds fairly well with the bone called the "epiotic." . . . It may be objected that the presence of an epiotic bone [tabulare] in the lizards is a far too primitive character, but we are now quite certain that the lizards are an exceedingly old group, probably dating from the Permian, and that they have not a few primitive characters,"¹ etc.

The condition of this bone in the mosasaurs is such that one might easily conceive that it is a compound bone formed by the outer part of the paroccipital and the tabulare fused together, though I no longer believe that any part of it is the paroccipital. It was Cope who insisted that the bone in the mosasaurs is the paroccipital only, a view that was vigorously combated by Baur. This view, that the bone is the tabulare, I have consistently held

¹ Williston, *Biol. Bull.* (1904), p. 190.

ever since, though it is only very recently that any other writer has accepted my contention. Three years ago I again expressed my opinion as follows: "I have long believed that the small element intercalated between the paroccipital and the so called squamosal of the lizards corresponds to the epiotics of the stegoccephs,"¹ etc.

In front of the parieto-tabulare arch the side of the parietal is concave and free, forming the upper, inner margin of a typical supratemporal vacuity. It was this free border, seen in two specimens, which convinced me originally of the presence of a temporal vacuity in the skull of *Araeoscelis*.

The relations of the *postfrontals* and *postorbitals* are shown in four specimens. The postfrontal is a small bone which forms the upper, posterior border of the orbit, extending forward on the frontal margin not quite to the middle. Below, near the middle of the postorbital, it unites by a slender squamous underlap with the slender postfrontal process of the jugal. In five different specimens this suture is seen, but more positive evidence is furnished by another in which the jugal had been separated a little distance from the postfrontal, showing the delicate striated sutural surface for their union. The postorbital unites with both postfrontal and jugal by a convex suture, which approaches near its middle very near the orbital margin. Above, the postorbital reaches narrowly to the parietal, back of the postfrontal. In one specimen these bones have been separated from the frontal and parietal, leaving the striate sutural surface free. Below, the somewhat thinned anterior part of the postorbital extends downward between the jugal and squamosal at least a third of the way to the lower margin of the arch. Although in one specimen the lower border seems to be complete, I cannot be quite sure of its extent. From this expanded anterior part the bone contracts to extend more and more slenderly very nearly to the tabulare, thus forming nearly the whole of the outer border of the temporal vacuity. Along its whole lower border it is suturally united with the squamosal. These relations are corroborated in so many specimens that there cannot be the slightest doubt on the subject.

¹ Williston, *Amer. Jour. Anat.* (1910), p. 82.

The *squamosal* is a flat and thin bone which fills out the broad expanse of the sides of the skull back of the jugal. It has a very slender connection with the outer border of the quadrate above, and extends downward very nearly to the cotylar margin. At its upper angle, just back of the hind end of the postorbital, it has a facet for union with the tabulare. Below, the bone forms nearly the whole of the lower margin of the arcade. I can find no evidence of a distinct quadratojugal; if such a bone was present it is so firmly fused with the squamosal as to be indistinguishable in any one of the four sides in which the squamosal is preserved nearly entire. In front the bone reaches forward to the hind border of the jugal in one case; in others the anterior part is deficient, so that I cannot be quite sure of the relations here of postorbital and squamosal. It is not impossible that my identification of tabulare and squamosal may be contested—there has been such a vast deal of speculation about the temporal arches that one must expect more—and that what I call the tabulare may be declared to be the squamosal and my squamosal the quadratojugal. But, inasmuch as such an interpretation will be speculation purely and impossible of proof, I am not disturbed by the possibility.

The *quadrate* is more or less exposed in three cases; in one it is nearly wholly exposed on the front side. It is expanded, somewhat fan shaped above, and is thinned. It is visible on the outer side narrowly behind the squamosal attachment. It articulates with the end of the tabulare above, with the paroccipital on the inner side, and with the squamosal on the outer side, as described for that bone. Just above the cotylar margin there is a free, concave surface, bridged over possibly by the lower part of the squamosal. If so, there would seem to be a small quadrate foramen here, arguing the presence of a quadratojugal bone. But I do not think that the evidence is conclusive. The quadrate stands somewhat obliquely, with the outer, gently curved, and thicker margin forming the posterior border of the temporal region; its anterior border is directed forward and inward, and is continuous with the posterior process of the pterygoid. Just how much of this part is pterygoid and how much quadrate I cannot say.

The *jugal* is well preserved in two specimens, completely so in one, with the postfrontal process broken away in the other; a third specimen shows the posterior process. It is a long, narrow bone, which borders the whole lower side of the orbit. It sends a short, pointed process backward to articulate below the front part of the squamosal. The process which is directed upward to meet the postfrontal and postorbital is broader, ending in a slender projection on the front side which overlaps narrowly the postfrontal in front of the postorbital. Posteriorly above it also meets the lower part of the anterior expansion of the postorbital. The anterior end extends nearly to the extreme front end of the orbit, bordering for a long distance the upper side of the maxilla. The bone forms the free margin of the arch back of the maxilla for only a short distance.

The *frontals* are moderately broad and rather long bones, evidently flat or gently concave between the orbits. In most specimens they are pressed more or less together, but, by excavating one of them, I have determined its precise shape. It forms the orbital margin for only a short distance between the ends of the postfrontal and prefrontal. The frontonasal suture is a little before the front end of the prefrontal.

The *prefrontals* are visible in part or wholly on four sides. They are large, triangular bones, projecting outward somewhat in front of the orbit. They extend back narrowly along the frontal margin to within a short distance of the anterior end of the postfrontals.

The *maxillae* are unusually broad bones for a Permian reptile. Each articulates with the nasal in front, excluding the lacrimal from the nares. It is more or less complete in four cases. It terminates posteriorly in an acute point a little before the hind border of the orbit, and is bordered to its highest elevation by the slender jugal. A small space is left between the end of the jugal and the prefrontal in which there may have been a small *lacrimal*, but this bone cannot be distinguished with certainty in any specimen.

Of the *premaxillae* I can say but little. In only one of the specimens can I detect any vestige of it. In one skull, however, the

mandibles are preserved in position with the maxillae entire, showing that the premaxillae must have been small, with not more than two teeth in each.

The *occiput* is clearly distinguishable in two skulls, and partially so in a third. It has a smooth declivity on each side between the angular median projection and the foramen magnum on the inner side, and the parietal arch on the outer side. The surface, descending nearly to the lower border of the foramen magnum, is clearly distinguishable from the dorsal surface and the tabulare, although no distinct post-temporal vacuity is visible; probably in life there was a small vacuity here, which has been obliterated by the depression of the arch. At the outer side the thin bone abuts against the distal end of the tabulare, and thus must come in contact with the upper end of the quadrate. I can distinguish no sutural divisions on this surface, though doubtless it must be formed by the supraoccipital, paroccipital, and exoccipital. I am very skeptical of some of the recent interpretations of the structure of the occipital region of certain American Permian reptiles. It cannot be said too emphatically that only under the most exceptional circumstances can sutures be determined with any degree of certainty from single specimens. The foramen magnum is large; the occipital condyle is hemispherical.

The details of the palate are less certainly determinable. There is an interpterygoidal vacuity, with low, conical teeth along the pterygoids and vomers in front. One specimen shows an indication of a median parasphenoid. The downwardly prominent portion corresponding to the transverse bone—if it be distinct—is armed with five conical teeth of a size nearly as large as those on the anterior part of the maxilla; this elevation joins the maxilla just back of the teeth. Back of these transverse rows of teeth there is an elongated basisphenoid, with a shallow cavity in the middle and a low basisphenoid tuberosity on each side at the end of a lateral elevation.

The teeth of *Araeoscelis* either are variable or the material that I have assumed to belong to a single species comprises more than one. Without better evidence to the contrary, however, I shall assume that the differences which they present, like those of the

skeletal bones, are merely ontogenetic or individual. Typically—that is, those adult skulls associated with the largest vertebrae, and doubtless belonging with the largest humeri and femora—there are fourteen teeth in the maxilla, with the shapes as shown in the illustrations (Fig. 3, *F, A*), that is, with the first four rather slender and of nearly equal length; the next four are a little broader at the base, though but little longer; with the ninth they increase in size, both in length and breadth, reaching the maximum in the twelfth; the thirteenth and fourteenth decrease a little in length. Possibly there is a smaller one beyond these, but if so, I cannot distinguish it. This is the condition in both maxillae in one specimen lying in the matrix, in which the teeth have not been injured in preparation. In another skull the number of teeth is the same, but the ninth to the eleventh are not noticeably larger than the preceding ones. In a third specimen, one of the larger ones, I count fourteen teeth in the maxilla, but the last three are small. Finally, in still another specimen, comprising only the maxilla, mandible, face, and anterior palatal bones, fifteen teeth are preserved in the maxilla, with an alveolus for at least one more, and probably alveoli for two more. These teeth, moreover are all smaller than in the other specimens and are of uniform size throughout. The teeth are all simple, without accessory cusps of any kind. They are somewhat wider at the base than long antero-posteriorly and are beveled on the inner side. They are somewhat flattened on the outer side and are obtusely pointed. They are thecodont or protothecodont.

This description in the main seems to agree with that given by Broom¹ of *Ophiodeirus*, though some effort is required to understand his description. One does not feel sure, for instance, what the antecedent of “it” is in the twentieth line of his description of the teeth, but I assume that it refers to *Ophiodeirus*. In the typical *Araeoscelis* it is the last or sixteenth tooth of the series which is smaller, while in *Ophiodeirus*, if I understand the description correctly, the fourteenth, fifteenth, and sixteenth teeth are smaller. He also described the teeth of *Ophiodeirus* as cuspidate; they are not at all so in *Araeoscelis*.

¹ Bull. Amer. Mus. Nat. Hist. (1913).

The question of the relationship of *Araeoscelis* to *Bolosaurus* has been raised by Broom in the paper cited. He believes that all three genera, *Bolosaurus*, *Ophiodeirus*, and *Araeoscelis*, are closely related members of the Bolosauridae of Cope. The genus *Bolosaurus* was originally described by Cope from a fragmentary skull, of which the only distinguishable character is found in the teeth. These are remarkable, formed as they are of a low crown, with a sharp principal and a low accessory cusp. The type specimens were later studied by Case who referred them to the Cotylosauria, as had Cope, and as did Huene also later. With these typical specimens Case later associated other imperfect ones discovered by himself, describing them, so far as his material sufficed, as *Bolosaurus striatus* Cope. With these later skulls Case provisionally associated a number of vertebrae and fragments of limb bones, but with no assurance, as he expressly stated, of their actual identity—they were merely found in the same bone-bed and he could refer them to no other known form. Had he followed the more usual rule of paleontologists he would have described them as new and left to others the problem of their identity! This caution, however, was not imitated by Broom, who referred all these remains to one species without question of possible distinction, notwithstanding Case's warning.

He distinguishes very properly the skeletal bones from *Bolosaurus*, of which nothing is known with certainty, under the name *Ophiodeirus casei* Broom, but recognized their relationship and possible identity with *Araeoscelis*. I had hoped that the time was past in vertebrate paleontology when genera and species were named on the mere possibility of validity. There can be scarcely a doubt that, aside from the skull, the bones described by Dr. Broom as of *Ophiodeirus casei* are those of *Araeoscelis gracilis*, and in much probability the discrepancy of the skull is due to error.

VERTEBRAE

The precise number of cervical vertebrae (Fig. 4, A, C, E) cannot be determined. The probability is seven, though there is the possibility of a larger number. The atlas has not been recognized, nor is its loss surprising, since the bones composing it must

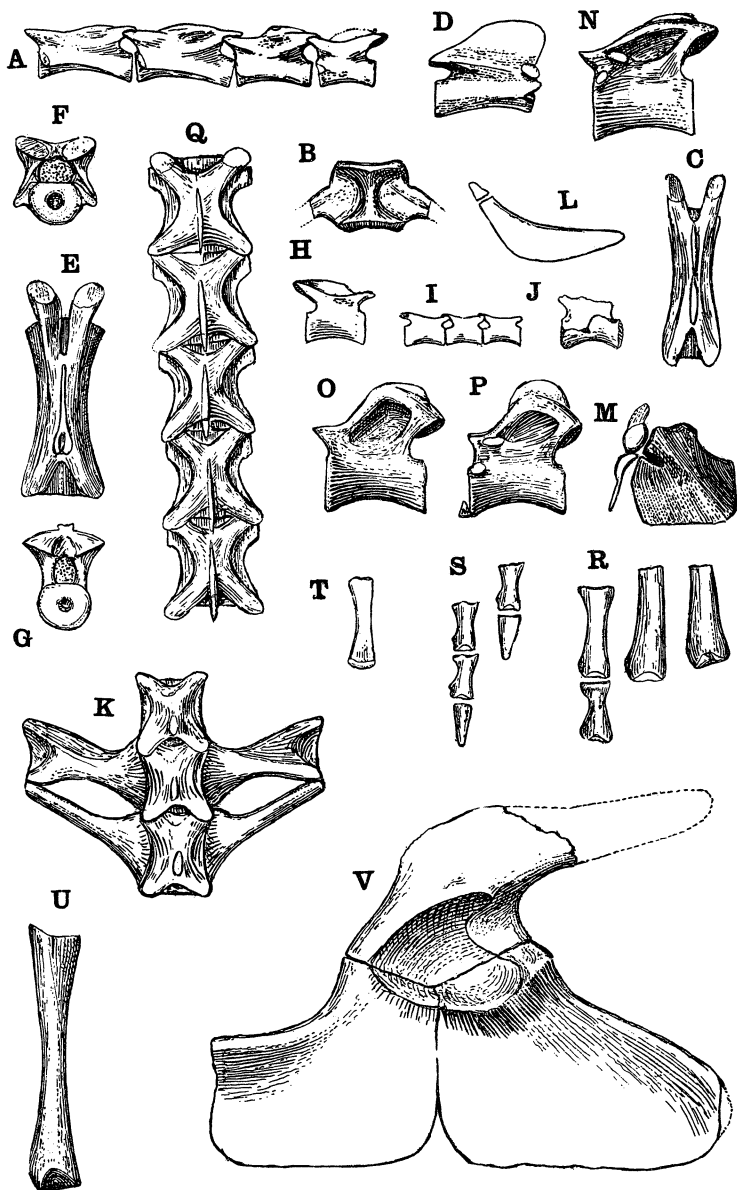


FIG. 4.—*Araeoscelis gracilis*: A, posterior cervical vertebrae of young, as connected in matrix; B, second caudal vertebra, from below; C, fourth or fifth cervical vertebra, from above; D, axis, from the side; E, median cervical, adult, from above; F, proximal end of same; G, distal end of same; H, median caudal, from the side; I, distal caudals, from the side; J, median caudal, from the side; K, first presacral and sacral vertebrae, not quite adult, from above; L, clavicle of half-grown animal; M, calcaneum, adult; N, dorsal vertebra, adult; O, lumbar vertebra, adult; P, anterior dorsal, adult; Q, series of anterior dorsals, adult, from above; R, metacarpals and phalanges of third, fourth, and fifth digits, as preserved in matrix; S, phalanges in positions as preserved; T, metacarpal or phalange; U, fourth metatarsal, adult; V, pelvis, adult, from the side. All enlarged one-half.

have been almost microscopical in size, and in none of the specimens has the neck been preserved complete.

A very perfect axis has been found among the loose material. It is shown in Fig. 4, *D*. It doubtless belongs with one of the larger, but not largest, skeletons; probably with the vertebrae shown in Fig. 4, *C*. It measures just 8 mm. in length, and differs markedly from any axis hitherto found in the American Permo-Carboniferous deposits. It has a rather high, thin spine of more than half the length of the centrum, its border sloping downward from above the middle of the centrum to divide into the two postzygapophysial processes. The anterior zygapophyses are unusually large, indicating a large atlantal arch. They are oval and are situated one on each side of the base of the spine, their faces looking upward and outward. The anterior end of the centrum is concave; it is rather narrow, and has an obtuse, keel-like process below; on each side there is a winglike process continuous with the front surface for the attachment of the cervical rib. The plane of the front end is at a considerable angle with the long axis of the centrum. The postzygapophyses are strong, but do not project far beyond the centrum. The centrum has a strong keel below in front, becoming linear posteriorly. The posterior surface of the centrum is nearly circular in outline, and is at right angles with the long axis. In the middle is a deep pit, which doubtless extends through the centrum.

Four posterior cervicals are associated in one specimen, belonging with one of the smaller skeletons. They are shown in Fig. 4, *A*. The first two of these are of nearly equal length; they are elongate and slender. On the side of the centrum in front there is a winglike projection with a facet, as shown in Fig. 4, *A*, for the articulation of a small, single-headed, cervical rib. Leading backward and downward from this facet there is a distinct ridge, which becomes obsolete before reaching the hind end of the centrum. In the middle of the centrum below there is a sharp, narrow keel. The prezygapophyses are more prominent than the posterior ones; their articular surface looks almost directly dorsad. The third vertebra of this series is not only shorter but it lacks the oblique ridge from the costal facet. The fourth is still shorter, and has

a tuberculiform parapophysis, but does not have a diapophysis on the side of the prezygapophysis, and hence must be considered a true cervical.

A second connected series of cervicals, of somewhat larger size, includes three elongated vertebrae, of nearly equal length. I cannot distinguish the posterior two from the anterior two of the preceding series, and the first of this series is scarcely different, save in having a little more pronounced spine on the posterior half of the arch rising directly above the level of the zygapophyses. The two series thus fix the number at not less than seven, four of which are much elongated, and the fifth only a little less so. This, however, does not preclude the possibility of a larger number of vertebrae in the neck. Among the free cervical vertebrae are four elongated ones of adult size, one of which is shown in Fig. 4, *E*, *F*, *G*. There are also several others like these, but of smaller size, one of which is shown in Fig. 4, *C*. They all have rudimentary spines, very thin, short, and low. In some, there is a very small cartilaginous surface on the upper margin. The cervical vertebrae were originally described by me as caudals, but the error was immediately recognized when the connected series were prepared.

Dorsals.—In the three specimens shown in Figs. 1 and 2 the dorsal series of vertebrae are complete and connected except that a few have been dislodged in the specimen presented in Fig. 2, *A*. Unfortunately in all three specimens the matrix has been removed from the ventral side, and it would be a matter of much difficulty now to clean the dorsal side and thus to determine the transition from the cervicals to the dorsals. Inasmuch as in two of these specimens the scapulae lie in relation to the nineteenth or twentieth presacrals, that number may be accepted as almost certain for the dorsal series.

Several other series of dorsal vertebrae showing the dorsal side have been prepared. A part of one of these series is shown in Fig. 4, *Q*, from above; and two isolated dorsal vertebrae are shown in Fig. 4, *N*, *P*, together with a more posterior one, a lumbar, in Fig. 4, *O*. The dorsals, as seen from below, are all rather slender; from above they appear less so, because of the overhanging arch. The centra are all more or less obtusely keeled below. An anterior

dorsal is shown in Fig. 4, *P*. In this vertebra the spine is more elevated than it is farther back; in much probability the spine is yet higher in the more anterior dorsals. The spine is thin, and has no tubercular projections of any kind. Another rib-bearing vertebra is shown in Fig. 4, *N*, with a less pronounced spine. The posterior zygapophyses overhang the centrum at a considerable elevation and there is, as in all, an excavation in the sides above. The articular processes for the rib form two surfaces separated by a distinct interval. The diapophysis is on the arch just back of the anterior zygapophysis; it projects but little or not at all beyond the margin of the zygapophysis. The facet for the capitulum is shown in several specimens as a small surface near the front end of the centrum, high up; whether it is on the arch or the centrum cannot be said, but it appears to be on the former. A series of five lumbar vertebrae, in all probability a part of the same skeleton as that to which the figured dorsals belong, differ in their somewhat greater stoutness, and in the entire absence of any diapophysial process or facet; the spine is also vestigial. One of these vertebrae is shown in Fig. 4, *O*.

Sacrum (Fig. 4, *K*).—The two sacral vertebrae and a connected lumbar were found in one specimen closely attached to the inner side of the left ischium. The sacral ribs on one side have been worked out fully, and on the other partly. The dorsal arch unfortunately had been injured somewhat. The sacral ribs are long, and those of the second vertebra very slender. They resemble so closely those of some lizards that it is needless to describe them further. As is seen, the first one has an expanded extremity and bore nearly the whole support of the ilium; the posterior one projects markedly forward.

Caudals.—Numerous caudal vertebrae are preserved isolated. One of a series of three proximal vertebrae is shown in Fig. 4, *B*, from below. The co-ossified ribs or transverse processes are elongate; none is preserved entire; they turn backward, as usual. More posterior caudals have tubercles on the sides for the posterior ribs. A yet more posterior caudal is shown in Fig. 4, *H*; it has a slight, thin spine on the posterior half, scarcely rising above the level of the zygapophyses. Three found attached in the clay matrix

are shown in Fig. 4, *I*. They are quite like the usual distal caudals of other reptiles. Although the entire number of caudal vertebrae cannot be determined, even approximately, the structure of the numerous isolated vertebrae preserved indicates decisively a long and slender tail. A median caudal of a young animal, shown in Fig. 4, *J*, is of interest because it is the only vertebra in the collection which shows any indication of the suture between arch and centrum.

PECTORAL GIRDLE AND EXTREMITY

Of the pectoral girdle nothing has been detected of the *inter-clavicle* in any specimen, and of the *clavicle* only one specimen has been discovered, that of a young animal not more than half adult size, as indicated by the associated long bones in the matrix. This bone is shown in Fig. 4, *L*, as it lies on the matrix in one plane. Its concave border is a little thickened, the convex thin; its scapular extremity is a little thickened, as shown by the section at the broken end. The bone has an unusual shape for a Permian reptile, as might be expected from the unusual shape of the scapula.

The *coraco-scapula* (Fig. 3, *C*, *D*) is of remarkable structure, so unlike anything I am acquainted with among reptiles that I was puzzled at first to interpret it. One complete specimen was found in an isolated nodule, overlapped on its coracoid border by a fragment of the opposite side. In order that the complete structure may be seen, this fragment has been sacrificed. The specimen seems to be quite perfect and undistorted, save that the upper part was smoothly broken and turned over the lower, as shown in Fig. 3, *A*, from behind. In Fig. 3, *C*, I have shown the whole bone as in one plane, though doubtless the upper part was curved strongly inward in life, perhaps more than I have indicated in the dotted line. The postglenoid facet is smooth, rounded, and gently concave; its face looks directly outward from the plane of the coracoid. The preglenoid facet of other Permian reptiles is divided into two very distinct processes, separated by a considerable space, in which there is a smooth, rounded border. There can be no possibility of error in this, since two other fragments, one of which is illustrated in Fig. 3, *E*, show the same peculiarities. Nor can

I find any trace of a supracoracoid foramen; a notch below the lower preglenoid process may represent the vacuity for the passage of the artery. An opening corresponding to the supraglenoid foramen seems to be present just above the supraglenoid articular surface. Apparently the suture distinguishing the coracoid in front is seen in a division across the bone, which I have indicated by a dotted line; but I cannot find the least trace of an anterior suture.

Doubtless the scapula proper must include all that part above the upper facet; possibly the lower preglenoid process is on the anterior coracoid, if there be such a bone in this scapula. At the upper end the scapula is rather narrow, with a thin front border, and a thickened posterior border. If the two coracoids met along the middle line, the blade of the scapula must have projected strongly forward. But that is improbable. Probably the two sides approximated each other only at the posterior end, leaving a large V-shaped interval between the anterior borders, partially filled out by the clavicles and interclavicle.

Humerus.—Three complete humeri are preserved free (Fig. 2). Two other complete ones, of a somewhat smaller size, are preserved in the matrix, associated with skeletal bones; and there are various other parts of juvenile humeri that were found in the clay matrix, portions of which have been lost. The articular head in the best-preserved specimen (Fig. 2, *E*) is oval in shape, and is not widely separated from the lateral process, which is much nearer the head than is usual in Permian reptiles. The bicipital fossa is rather shallow. The distal extremity is thin and flat, and is only moderately expanded on the ulnar side. The entepicondylar foramen is small, and is bridged over by a very delicate bar of bone, so delicate that it has been lost in all our specimens. Indeed, so thin is the broken edge left above the foramen that for a time I was in doubt as to whether it was not merely a notch. I am now convinced that the foramen was closed in; nevertheless it seems to be obsolescent. On the radial side there is an ectepicondylar foramen, quite as in modern lizards, formed by a slight bridge over the end of the ectepicondylar groove in the adult humerus, but wholly wanting in the juvenile specimens. The capitellum is well formed, as is also the

trochlear surface for the ulna. Both are small, but the joint here was evidently unusually compact and strong.

The planes of the two extremities of the humerus are turned nearly at right angles with one another. One would not recognize the figure given by Broom of the humerus of *Ophiodeirus* as that of an allied animal even, much less as that of *Araeoscelis*, were it not for the statement in the text that the two ends of the specimen, as figured, did not connect with each other. He thought that little was missing and figures the two ends in the same plane, though an examination of the humerus of *Araeoscelis*, as figured by me, should have convinced him of his error. As a matter of fact, taking as indices the two ends as figured, a slender cylindrical piece of the shaft 12 mm. in length was missing, giving a total length of about 50 mm. for the whole humerus, a trifle less than that of the adult humeri here figured. With these corrections his figured humerus may well be that of *Araeoscelis*.

There are no complete specimens of *radii* or *ulnae* preserved, though there are several partly complete. There can be scarcely a doubt that they were as long as the humerus. In two specimens the proximal ends are preserved in relation with the humerus, and two others have the distal ends preserved in relation with the carpus. Both bones are of equal size and are nearly straight. The radius has a cupped surface at the proximal end and a moderately expanded distal end. The ulna has a moderately produced olecranon; the distal end is a little less broad than that of the radius; there is no articular surface for a pisiform.

Carpus (Fig. 2, *F*).—The carpus and hand of *Araeoscelis* are so unlike those of other known contemporary reptiles that careful study was necessary for their interpretation. Fortunately, however, the material is good, and pretty nearly complete, consisting chiefly of two specimens, both with the carpals nearly all in position, together with the distal ends of the epipodials and the proximal ends of some of the metacarpals. The better of these specimens has the bones cemented together in a nodule that was inclosed in clay, which was cleanly washed away, leaving the bones visible. The wrist was compressed a little and flexed, so that the radius and ulna had slipped backward and downward, carrying the radiale

with them. Nor is there anything left in this specimen of the first and second metacarpals and the first carpale. The second specimen includes the epipodial and mesopodial bones and the proximal ends of the first and second metacarpals; the intermedium is not visible, possibly it is lost. There is also much more of the metapodials than in the other specimen, though none is complete. In a separate piece of clay at least three fingers were lying in position, but only the three metacarpals and some of their phalanges were preserved in place. These have been added to the figure made from the first specimen in dotted lines. The three specimens are the same or nearly the same size.

The *ulnare* is a stout, thick bone, which forms half of the articular surface for the ulna. It rests only slightly on the fifth carpale, though more than is shown in the figure, since it underlaps it to a small extent. At its lower, outer angle there is a small notch, all that seems to represent the perforating foramen. Its outer border is straight, and joins the inner border of the intermedium closely. The *intermedium* is a cuboid bone, a little wider below than above, with a considerable concave articular surface at each end, that of the proximal end continuing smoothly the ulnar articular surface. The *radiale* is seen only from the proximal side, as it lies back of the other carpal bones at the ends of the radius and ulna, the ulna partly rotated on its long axis. This surface shows an excavation where it partly covered the centrale. On the ulnar border there is a distinct notch between it and the intermedium that is puzzling. Lying by the side of the radiale there is a small nodular bone which must be either the first carpale or the first centrale; I have dotted it as the centrale. The *centrale* is a narrow bone with peculiar relations. At its inner side it articulates with the outer angle of the fifth carpale. The fifth carpale is also unlike that of any other Permian reptile that I know in its large size and relations with the fourth carpale, which it excludes from the proximal bones. The fourth carpale is small. It interlocks with both the centrale and the fifth carpale. The third carpale has a flat, rectangular anterior surface, a little longer than wide. It articulates above with the outer end of the centrale, and on each side with an adjacent carpale. The first carpale is a small bone.

The *fingers* are remarkable, so far as they are preserved. The great size of the ulnar ones over the radials suggested at first the possibility of error in their determination. As shown in the illustration, the unbroken lines represent bones of the more complete specimen, while those shown in dotted lines are taken from the other two specimens as they lie in place. There can be no legitimate doubt of the phalangeal formula, 2, 3, 4, 5, 3. Not a few slender phalanges are preserved loosely, belonging in the fingers. The claws are elongated and sharply pointed.

PELVIC GIRDLE AND EXTREMITY

Pelvis (Fig. 4, V).—The more or less complete pelvis is preserved in three different specimens. In addition, there are two isolated ischia preserved in small nodules; one of these is of a young animal, the other of a nearly full-grown one, though a trifle smaller than the largest. These two small ischia have been used to complete the drawings made from an adult specimen. The pubes in the three associated skeletons shown in the figures are determinable in all details. The ilia are concealed in the pelves associated with the vertebrae, but there are two incomplete ones that were found free in the clay, in perfect preservation, save for the loss of the greater part of the posterior process.

The ilium, so far as it is determinable, shows no peculiarities of note to distinguish it from the common pelycosaur type, especially that of the poliosaurids. It has a rather slender posterior process, like that of *Varanosaurus*. Nor is the ischium at all peculiar; it is, indeed, of the form of all the ischia known of the American Permian, meeting its mate in a broad symphysis, and doubtless forming a more or less spout-shaped orifice to the pelvis. The pubis, however, departs markedly from the universal pelycosaur type, that observed in *Dimetrodon*, *Sphenacodon*, *Varanosaurus*, etc., agreeing rather better with that of *Casea*. In the fully adult specimens it meets the ischium in a nearly complete sutural union, leaving no puboischiadic vacuity, or a very small one, such as is always found in the true pelycosaurs. It is subquadrate in shape, with its superior outer margin somewhat thickened and emarginate, but not forming a spout-like anterior

projection. Broom compares the pelvis of *Ophiodeirus*, or his so-called *Bolosaurus*, with that of *Poecilospondylus*, but restores the latter wrongly. All the Poliosauridae, as indeed all of the Pelycosauria in the narrower sense, have a very characteristic pubis, standing horizontally far in advance of the true pelvic brim. I have seen the type specimen of *Poecilospondylus* and know that it is intimately allied to the genus I have described as *Varanosaurus*¹ but which is not congeneric with the genotype. Indeed, there is no more characteristic bone in the true Pelycosauria than the pubis, an element that I have relied upon, perhaps unduly, as a determinant of the relationships between the Sphenacodontidae and Poliosauridae.

Numerous juvenile or incomplete *femora* (Fig. 5, *A-D*) are represented among the free material found in the clay, but there is only one complete femur of an adult, with parts of three others. It is the longest bone in the skeleton, measuring about $2\frac{1}{2}$ inches in length. In front view the bone is nearly straight, with a long, cylindrical shaft and only moderately expanded extremities. In side view the bone is shaped much like the italic letter *f*, with the concavity above, the convexity below, on the front side. The head is stout and rounded, with its articular surface almost wholly at the extremity. The trochanter, a rather thin plate, springs inward and backward nearly at right angles, a little below the head, and continues as a thin edge, winding about the shaft till it reaches the middle, a little above the middle of the bone, and then continues as a *linea aspera* to the lower third, where it becomes obsolete. The tibial condyle juts inward, forming a right angle. The tibial surface is narrow, but connects broadly with the fibular surface. The two surfaces together make an angle of nearly 45 degrees with the long axis of the bone.

Tibia and fibula.—The tibia and fibula (Fig. 5, *E-I*), like the radius and ulna, are remarkably slender bones, fully as long as the femur. No free specimen of either bone is preserved entire, though one of each, in all probability those belonging with the femur

¹ The recent descriptions by Broili and Watson of the genotype of *Varanosaurus*, *V. acutirostris*, disclose, as I suspected, generic differences from the species *V. brevisrostris* Williston. I therefore propose the generic name *Varanoops* for the latter.

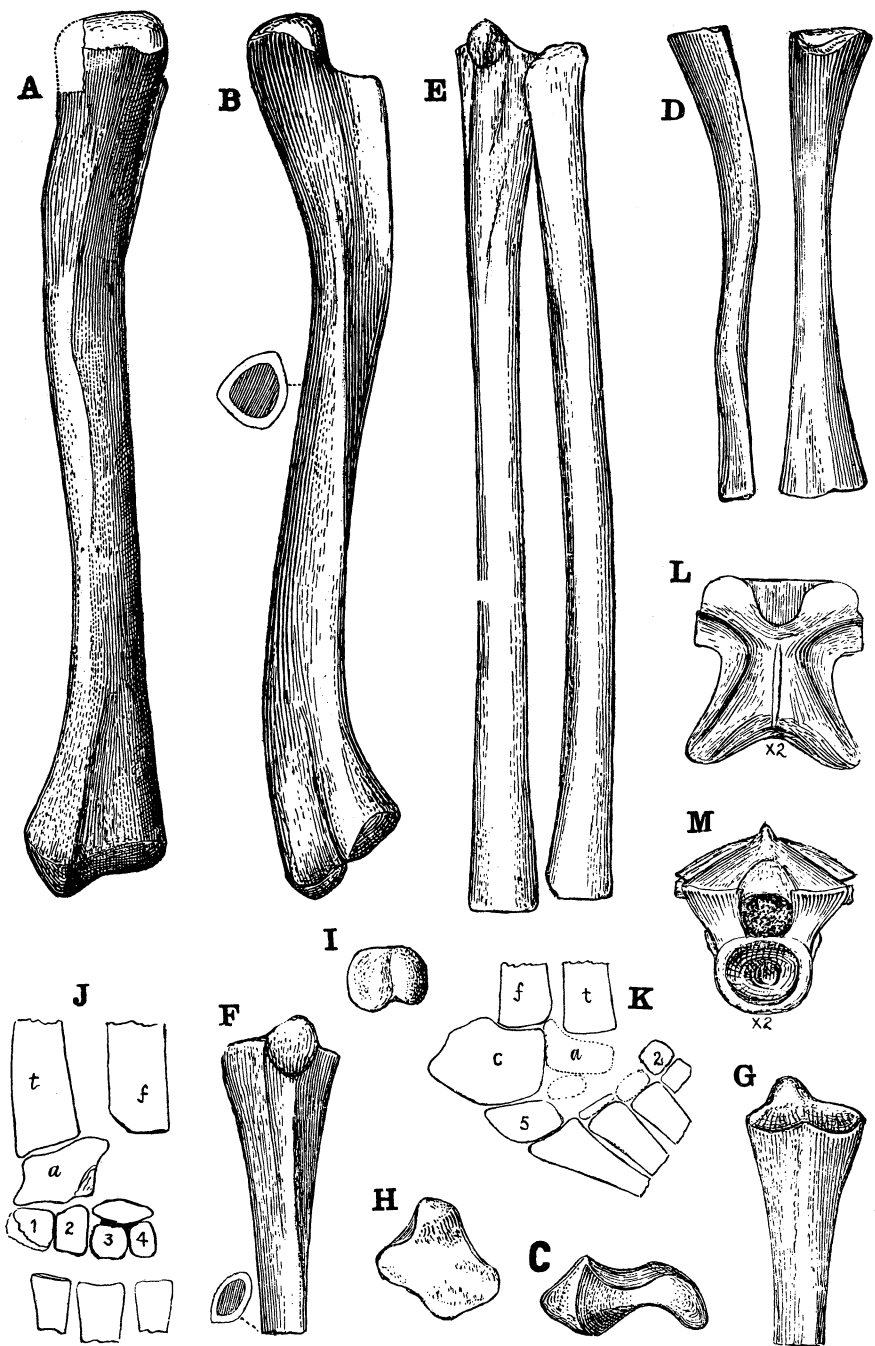


FIG. 5.—*Araeoscelis gracilis*: A, right femur, obliquely from above, adult; B, the same, obliquely from tibial side; C, distal end of same; D, femur of half-grown specimen, from side and front; E, tibia and fibula, adult, from the front; F, right tibia, proximal end, from the front, adult; G, the same, from behind; H, the same, from above; I, fibula, distal end; J, part of tarsus of Fig. 1, B; K, part of tarsus, immature; L, dorsal vertebra, from above; M, the same, from the front. All except L and M enlarged one-half.

that I have figured, are very nearly complete. In Fig. 5, *E*, the two bones are shown as completed from these and other specimens, aided by the complete specimens of a little smaller size shown in the associated skeleton of Figs. 1 and 2. The tibia (Fig. 5, *E-H*) is considerably expanded above, and has a prominent cnemial ridge ending in a rounded, rugose, cnemial crest above, for the attachment of what was evidently a strong quadriceps extensor ligament. Its upper surface is gently concave and fits very perfectly the distal articular surface of the femur. Its shaft is nearly straight and nearly cylindrical, or a little flattened. Its lower extremity is but little dilated, and its end is squarely truncate. The fibula is a little more curved, but scarcely differs in size from the tibia. Its upper end is moderately dilated on an oblique plane. Its lower extremity, as shown in Fig. 5, *A*, is nearly cylindrical, its articular surface distinctly divided into two facets, the one on the tibial side for articulation with the astragalus, a little narrower than the calcaneal, and rounded.

Foot.—The *tarsus* (Fig. 5, *J, K*), more or less complete, is preserved in two specimens, and in part in a third. Of one of these the bones are shown as they lie at the ends of the tibia and fibula in Fig. 5, *B*, and as brought as nearly as possible into their articular relations in Fig. 5, *J*. The tibia in this illustration is shown partly from the side and has apparently undergone a slight external curvature, though it is possible that this curvature is natural, and that I have represented the shaft in Fig. 5, *E*, too straight on the lower part. The astragalus is a small cuboid bone, very different in form from that of other known Permian reptiles, in that I can detect no surface on the inner side for the arthrodial articulation of the tibia. Its articulation with the tibia seems to have been firm and close, with not much motion. Lying at the outer side of this bone is a smaller one which can be interpreted only as a centrale of small size, articulating with the third and fourth tarsalia and probably somewhat with the astragalus. This is a rather unusual position for the centrale, but it seems certain that such were its relations. The first two tarsalia are relatively large, the third and fourth small. The fifth tarsale and the calcaneum are missing in this specimen.

A second specimen, in a small block of matrix belonging with a smaller animal, has the bones in the positions shown in Fig. 5, *K*. The distal ends of the epipodals, the calcaneum, fifth tarsale, and first tarsale are shown very clearly in the outline, but in their excavation from the hard matrix the surface of the tarsal bones has been somewhat injured. Crowded in the space below the tibia the bones of the external side of the tarsus are more confused and injured; but they confirm, so far as they can be deciphered, the arrangement shown in Fig. 5, *J*. The calcaneum (Fig. 4, *M*) is shown very perfectly and undistorted in a free specimen found in the clay. The heel is distinctly produced and has a slight cartilaginous thickening on its border for the Achilles tendon. The tibial surface shows very distinctly the notch for the perforating foramen. Elsewhere the borders are rather thin, save that for the articulation with the fibula. The fifth tarsale is shown very completely. It is of unusually large size, filling out the space between the calcaneum and the fifth metatarsal. All these bones in this specimen lie evidently in a natural position, the bones closely articulated.

Only four metatarsals are preserved together in any specimen, though the presence of the first tarsale would seem definitely to indicate the presence of the full five. It is also evident from these that the bones of the fibular side were stronger than those of the tibial, corresponding to those of the front feet, though the difference is not so great. Parts of three digits are shown in Fig. 4, *R*, as they were preserved in a small mass of clay. Doubtless the whole foot or the greater part of it had been present, but only these were recovered, though it is probable that the bones shown in Fig. 4, *S*, belong with the same specimen. The single metatarsal of adult size shown in Fig. 4, *U*, seems to correspond in its proximal and distal ends with the fourth; and it is evident that the digit showing the two phalanges of Fig. 4, *R*, is the fifth. The phalanges shown in Fig. 4, *S*, are in all probability the distal ones belonging with the two metatarsals shown in Fig. 4, *R*, that is, of the third and fourth digits, and that two proximal ones of each digit were ones probably corresponding in size pretty well with those of the fifth toe of Fig. 4, *R*. On these assumptions the feet may be restored with much probability.

RELATIONSHIPS

Araeoscelis is the first paleozoic reptile in which a typical upper temporal vacuity has been definitely recognized. The Proganosauria, only, from an approximately equivalent age, have been accredited by Huene with a single, upper temporal vacuity, and doubtless correctly, but its boundaries and position have not yet been certainly determined. Inasmuch as great importance has been attributed to the number and boundaries of these openings in the relationships of reptiles, it will be well to discuss briefly all those forms in which only an upper opening is known or supposed to be present. Various theories have been proposed concerning their origin and relationships, but in my opinion they are as yet for the most part speculations, or at the most hypotheses. Attempts to base a primary classification of the order chiefly on the number of temporal openings so far have not been very successful. The most meritorious of these attempts is that of Professor Osborn, which, though it can no longer be accepted as the true solution of the reptilian phylogeny, did much to place the classification of reptiles on a more secure basis; notwithstanding its faults, its merits are obvious. All students of the order are in practical accord as regards the phyletic relationships of the double-arched forms. It is only concerning those groups in which there is but a single opening that grave doubt and uncertainty yet remain. The single vacuity, when present, is so inconstant in its position and in its boundaries that one is seldom certain whether it is the upper, or lower, either or both; or, indeed, as Watson thinks, in some cases neither!

The following groups of reptiles, more generally considered to be orders, have a single temporal vacuity on each side: Ichthyosauria, Sauropterygia, "Pelycosauria," Placodontia, Therapsida, Squamata and, if Huene is correct, the Proganosauria. Of these the Pelycosauria and Therapsida may at once be dismissed in any discussion of the relationships of *Araeoscelis*, since the opening, whether upper or lower or neither, has such different relations and boundaries as to preclude any immediate phyletic relationships. And, of the others, the Sauropterygia can have only a remote relationship and may be dismissed from the discussion. In addition

to these, some poorly known forms that have long been classed with the rhynchocephalian reptiles, under the assumption that any primitive reptile in which the temporal region was unknown probably was allied to *Sphenodon*, show such possible or probable resemblances to *Araeoscelis* as to merit consideration.

Squamata.—I have no hesitation in saying that the skull and skeleton of *Araeoscelis* present distinctively primitive characters of the *Squamata*, to such an extent indeed that I believe the genus has a definite phylogenetic relationship with the order. In fact, as far as the skull is concerned, all that seems necessary to convert *Araeoscelis* into a primitive lizard is the erosion of the lower part of the squamosal bone until only a slender rod is left along the under side of the postorbital, and the development of streptostyly in the quadrate, which would necessarily ensue with the loss of the support of the squamosal. The quadrate is supported quite as in the lizards by the tabulare and paroccipital, in conjunction with the squamosal. The quadrate itself retains some of its primitive characters in its moderately expanded upper end, which, however, is much less in extent than in other known contemporary reptiles. It is visible in part from the side, and fully so from behind. The postorbital is peculiar and unlike that of other known reptiles in that it takes no part in the formation of the posterior border of the orbit. In conjunction with the postfrontal it is quite like that of the mosasaurs and lizards in its extension backward nearly to the tabulare. Among mosasaurs I have seen indications of a sutural division of the "postfronto-orbital," and I have little doubt that the bone is really composed of the two elements. If it be really only a single bone, it must be the postorbital, not the postfrontal. In the reduction of the lacrimal to a small or vestigial bone we have another pronounced lacertilian character, never before observed in the earliest reptiles.

Unfortunately I have been unable to determine all the details of the palate. Although teeth are not known on the vomers¹ of

¹ For some years I was inclined to accept the conclusions of Broom that the so-called vomers of most reptiles were not homologous with the vomer of mammals, which represented the parasphenoid; and to adopt the name he proposed for them, prevomers. The more recent studies of Gaupp, Fuchs, Versluys, and Terry throw grave doubt, to say the least, over these conclusions. I therefore return to the use of the term "vomer."

squamate reptiles, their presence in *Araeoscelis* is only what would be expected in a primitive lizard. Nor is the presence of teeth on the transverse bone (if it be distinct) a character to which any weight can be attached. Though no lizards have such teeth we may be sure that their ancestors had them.

In the structure of the skeleton of *Araeoscelis* there is very little that would not confidently be expected in the primitive lizard. The ribs of the neck and lumbar region are single-headed in the strictest sense, not holocephalous, as in the cotylosaurs, and they articulate exclusively with the centrum. In the dorsal region they are dichocephalous, but the head and tubercle are close together, separated only by a short emargination. The head is articulated, unlike the condition in contemporary reptiles, high up on the side of the centrum near the front end, the tubercle to a short diapophysis on a level with and just back of the anterior zygapophyses. The fusion of these two articulations, or, what is more probable, a loss of the diapophysis, which actually occurs in the lumbar region, would make the rib attachment typically lacertilian. I am quite sure that the primitive lizards had dichocephalous or holocephalous ribs, that is, capitular and tubercular articulations. *Araeoscelis* offers a rational explanation of the way the very peculiar rib attachment of the Squamata arose.

The pectoral girdle shows certain peculiarities not known among the Squamata, especially the separate articular facets in front of the glenoid facet, and the possible absence of the supra-coracoid foramen. The distinction of the coracoid is not quite certain, though the dotted line of the figure represents what seems to be a real sutural division. I have urged that the posterior coracoid bone has been lost in all modern reptiles; that such a bone was present in the ancestral lizard is quite certain.

In the anterior extremity the presence of a distinct ectepicondylar foramen, quite as in the lizards, is suggestive, at least, of genetic relationships; and there is also a suggestion that the entepicondylar foramen was obsolescent. The structure of the feet is unlike that of the contemporary reptiles in the elongated calcaneum and reduced astragalus. The pelvis is plate-like, without a decided pubo-ischiadic vacuity; but no other kind of a pelvis could be expected in the primitive lizards.

The elongation of the cervical vertebrae was clearly a specialization and not an ancestral character; but aside from this and the peculiar scapula, I can see nothing in the entire skeleton that might not have been confidently predicted in the ancestral lizard. It may be objected that the thecodont, or more properly protothecodont, teeth were an aberrant character; that the lizard ancestor must have had, like the living ones, acrodont or pleurodont teeth. On the contrary, I believe that the teeth primitively in the Squamata were protothecodont, which, by the loss of the parapet of bone on the inner side of the maxillae, and the anterior part of the coronoid, became pleurodont. Moreover, the teeth in the mosasaurs are attached in shallow cavities. In Fig. 3, G, I give a sketch drawing of the skull of *Opetiosaurus* Kramb., the earliest known skull of a squamate reptile, from the uppermost part of the Lower Cretaceous. The figure was made by me from the type specimen in the Munich museum, and differs somewhat from previous ones by Kramberger and Nopsca.

Proterosaurus.—There are certain marked resemblances between *Araeoscelis* and *Proterosaurus* which may, and probably do, indicate genetic relationships. Unfortunately much doubt remains as to the structure of the skull in this genus, notwithstanding the numerous specimens which have been studied during the past two centuries. Seeley's interpretation of the skull structure of *P. speneri* has been received with considerable doubt by later students. I have examined the specimen on which he based his results chiefly, preserved in the collection of the Royal College of Surgeons, but could make little of it; my examination, however, was brief, and without the aid of Seeley's paper. Nevertheless, I am inclined to the belief that his interpretation of the elements will eventually be found to be approximately correct. He figures the temporal region as open at the sides of the narrow parietals. If it should be found that the side was largely covered below by the squamosal, leaving a vacuity above, the structure would be essentially like that of *Araeoscelis*.

There is certainly as much justification for this hypothesis as there is for the one usually accepted, the presence of two temporal arches, for which I can see no evidence whatever. Nevertheless,

it was on this assumption and the equally unjustified assumption of a superior temporal vacuity in *Paleohatteria*, that these two genera and others even more indeterminate have been almost unreservedly classed either among the Rhynchocephalia or as a group of the Diaptosauria, of which the true Rhynchocephalia are another member. As I have elsewhere said, *Sphenodon* and the Rhynchocephalia have been, in the past, a cloak which has covered a multitude of taxonomic and phylogenetic sins. We have tried to trace all reptiles back to a primitive double-arched condition, on the assumption that *Sphenodon* is a very primitive reptile. It now seems more than probable that a single perforation of the temporal roof was the more primitive condition among reptiles, and that the Squamata are, in this respect, more primitive than the Rhynchocephalia. It has been assumed, indeed, that the Squamata themselves were derived from a primitive double-arched condition by the loss of the lower arcade, an assumption that in itself would seem to be improbable. Is it reasonable to suppose that the quadrate lost its fixity and became streptostylic suddenly, which would necessarily have been the case by the final loss of the quadratojugal arch? It would be far more reasonable to suppose that the gradual loss of a large squamosal, such as is found in *Araeoscelis*, permitted the gradual acquisition of streptostyly.

Seeley also figures a small antorbital vacuity in *Protorosaurus*, but with doubt; there is certainly none such in *Araeoscelis*. The lacrimal, according to Seeley, is small in *Protorosaurus*. So far, then, as I can see, there is nothing known in the skull of *Protorosaurus* that would prevent the immediate association of the genus with *Araeoscelis*.

In the skeletal structure *Protorosaurus* shows some remarkable resemblances to *Araeoscelis*: in the elongated cervical vertebrae, in the attachment of cervical and dorsal ribs, and in the general hollowness of the bones of the skeleton. These characters, in connection with the probable, or at least possible, resemblances of the skull, are, I believe, more than coincidences; they are genetic, not homoplastic.

Unfortunately little is known of the structure of the girdles in *Protorosaurus*. The vertebrae show distinct differences in the

elongation of the spines and in the reduced number of dorsals, though I think that the last-mentioned character is doubtful. The limb bones are not so much curved as in *Araeoscelis* but the epipodials are nearly as long as the propodials. Von Meyer also states that there are no epicondylar foramina in the humerus, and Seeley does not figure or mention any. The presence of a small ectepicondylar foramen, however, might easily have been overlooked, and I suspect that a close examination of adult specimens will disclose its presence. The bones are all very hollow as in *Araeoscelis*.

Kadaliosaurus.—There also seems to be much probability of a close genetic relationship between *Araeoscelis* and *Kadaliosaurus*, as shown in the skeletal bones in the absence of all knowledge of the skull. I had the pleasure of studying the type specimen of *Kadaliosaurus* the past year at Leipzig, thanks to the kindness of Drs. Stille and Krenkel. So far as the shapes of the limb bones and vertebrae are concerned, they seem almost identical with those of *Araeoscelis*. There is, I am convinced, an ectepicondylar foramen in the humerus, as Credner thought; there was probably also an entepicondylar foramen, though its existence cannot be proved, because of the loss of the ulnar border in the impression of the humerus, where the foramen should be. That the two genera are closely related I have little doubt, though it is hazardous to express a very decided conviction in the absence of any knowledge of the skull. *Kadaliosaurus*, however, differs generically in the structure of the long bones. I convinced myself thoroughly of the statement of Credner that the bones are not hollow, but are composed of cancellous tissue; the ribs, however, like those of *Araeoscelis*, are hollow. There is, also, a strong armature of ventral ribs, not the slightest indications of which have been observed in *Araeoscelis*. Further speculations as to the relationships of the two genera will be idle until the skull of *Kadaliosaurus* is discovered; the characters, so far as they are known, ally the two genera closely.

Paleohatteria.—This genus has long been associated with *Protorosaurus* as a member of the Protorosauria, or Rhynchocephalia, on the assumption of two temporal arches. We have seen how small was the justification for the assumption in *Protorosaurus*

and *Kadaliosaurus*; there is even less for *Paleohatteria*. We have tried to make every doubtful form in the past related to *Sphenodon*; even *Procolophon*, a true cotylosaur, has been placed in the same group, as a member of the Diaptosauria. As a matter of fact, *Paleohatteria* is not intimately related to the primitive rhynchocephalian stem, but is more closely allied to the so-called Pelycosauria, or even to the Proganosauria, as Baur first located it. I had the privilege, also, the past year, of studying the type specimens of *Paleohatteria* in Leipzig. Unfortunately some of the specimens had been loaned at the time of my visit to the museum, but the ones showing most conclusively the skull and skeletal structure were available. The results of my observations it will be worth while to reproduce here, though not immediately pertinent to the present subject. The skull, as shown in Credner's Plate XXIV, Fig. 3, is in my opinion preserved in a more natural profile than is any of the others, and is, I believe, more complete. The outline as I traced it is more complete and perfect than Credner figured it. The lower temporal opening is definitely shown, as are also the relations of the bone marked *sq* (quadratojugal?). Under the most careful scrutiny with a lens I could find no evidence of an upper vacuity. Neither do I believe that there is evidence of sclerotic plates in the orbits, though I did not see all the specimens.¹ The skull is rounded posteriorly, not projecting, as Jaekel has figured it. There is nothing in this specimen to suggest an upper temporal vacuity, nor could I find such evidences in any other specimen available for study. I could not distinguish the sutures between the prefrontal and lacrimal in any specimen; the lacrimal is certainly longer than Credner figured it, and it may have reached the nares. The upper surface of the skull, as stated by Credner, is distinctly rugose.

Credner's figures (Plate XXIV) of the scapula and coracoid are erroneous. The two are in close relation, but with the division visible (Fig. 6). The scapula seems to be somewhat longer than is visible, the upper end hidden below the humerus. The lower

¹ It has generally been assumed that the presence of sclerotic plates means aquatic habits, the fact being overlooked that there are not a few purely terrestrial lizards in which the sclerals are highly developed.

end is expanded, as in the allied American reptiles. The coracoid lies over the stem of the clavicle, and in all probability is composed of the anterior element only, which is the case with the numerous known scapulae coracoids of *Varanoops brevirostris*. The clavicle was represented by Credner as a slender rod, without designation; its shape is like that of *Ophiacodon*, and it lies in articulation with the interclavicle and the upper front margin of the scapula. I thought that I recognized the usual supracoracoid foramen in the impression of the coracoid, but in this I may have been mistaken. The outline of the coracoid is clearly shown on both sides of this specimen. The outline of the front border of the scapula is also clearly apparent, broadly convex below, gently emarginate above.

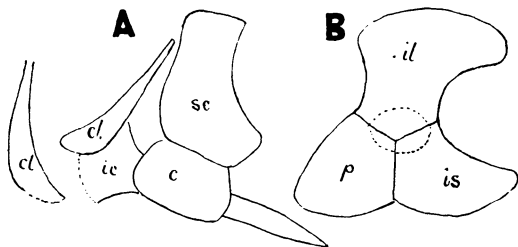


FIG. 6.—*Paleohatteria longicaudata* Credner: A, pectoral girdle, in part; B, left pelvic bones: *sc*, scapula; *c*, coracoid; *ic*, interclavicle; *cl*, clavicle; *il*, ilium; *is*, ischium; *p*, pubis.

In fact, the structure throughout of the pectoral girdle is like that of *Varanoops brevirostris*, or as it would be in an immature specimen of that species. The ribs are holocephalous, like those of *Ophiacodon*. The humerus in this specimen is turned outward, not inward,

and only an entepicondylar foramen is present. There are not more than three pairs of sacral ribs. In much probability the number of presacral vertebrae is twenty-seven, the constant number in the Pelycosauria in the more restricted sense. In brief, *Paleohatteria* is in every respect a member of the Pelycosauria (*sensu latiore*), of which it represents a family, Paleohatteriidæ (Baur), of co-ordinate value with the Poliosauridæ or Sphenacodontidæ.

Pleurosaurus (*Acrosaurus*).—This genus has generally been classed with the Rhynchocephalia in the narrow sense, notwithstanding the fact that it has but a single temporal opening, a fact that has previously been known and definitely confirmed by Watson. I had the pleasure of studying the excellent material of this genus preserved in the Munich museum, for which my thanks

are due to Dr. Broili. I reached the decided conviction that *Acrosaurus* is merely the young of *Pleurosaurus*. Of course the presence of a single upper temporal vacuity excludes the form decisively and absolutely from the Rhynchocephalia or Diaptsosauria, even. Whether or not it is intimately allied to *Araeoscelis* and *Protorosaurus* I shall not presume to say; but certainly its claims to such relations are vastly greater than those with the rhynchocephalian forms.

Proganosauria.—If Huene is correct in the attribution of a single upper temporal vacuity to *Mesosaurus* (and I believe that he is, notwithstanding the imperfect material that is in the collections of the skull of this genus), there may arise a question of the relationships between it and some of the forms I have briefly discussed. So far as the skeleton of the proganosaurs is concerned, it is simply an aquatic modification of the primitive cotylosaurian, or better, pelycosaurian type. Here, also, until the more precise structure of the skull is known, speculation is idle. The order Proganosauria may be accepted until it is proved that it has no claim for independent existence.

Ichthyosauria.—The origin and relationships of the Ichthyosauria have long been an unsolved problem, but little nearer solution today than it was a score of years ago, notwithstanding the brilliant discoveries of Dr. Merriam. On the strength of its generalized characters it has been associated with the rhynchocephalian type, as a member of the double-arched division of reptiles, under the hypothesis that the lower vacuity was secondarily closed by the encroachment of the orbit. More recently Huene has urged that its relationships are nearest with the Proganosauria, and with much reason. This much can be said: If all the known reptiles having a distinctive upper temporal opening have arisen from a single ancestral type, that is, are monophyletic, then the ichthyosaurs must be more closely related to the Squamata, *Protorosaurus*, and Proganosauria, than to any other known reptiles. This much I believe: The Ichthyosauria are of very primitive origin; they have never possessed a lower temporal vacuity; the two bones of the temporal region, variously known as supra-temporal and squamosal, point to a direct origin from the stego-

crotophous reptiles, provided these bones are not both identical with those I call the tabulare and squamosal in the lacertilians and *Araeoscelis*. If they are identical, then the two phyla may have originated together.

The problem remains, What shall be done with *Araeoscelis*? To throw it into a common receptacle with *Dimetrodon*, *Edaphosaurus*, and *Casea* may be an easy way to dispose of the genus, but it is hardly scientific. Some classification, even the most conservative, it must have; and while I am vigorously opposed to the still more reprehensible practice of giving every form that is hard to understand a new group name, it is evident that to place *Araeoscelis* with the Pelycosauria is to increase the confusion.

I have urged that the resemblances of *Araeoscelis* to the Squamata would justify its inclusion in that order as a suborder, under the name Araeoscelidia, co-ordinate with the Lacertilia and the Ophidia. And I believe that will be its final disposition under some subordinal designation. But it seems to me that the relations with *Protorosaurus* and *Kadaliosaurus* are too definite, too pronounced, to warrant their dissociation. I would therefore propose to unite these three genera, together with, provisionally, *Haptodus* and *Callibrachion*, under the order Protorosauria of Seeley, and place the order immediately before the Squamata in any serial classification of reptiles.

RESTORATION

The restoration of the skeleton shown in Fig. 7 is based upon the material described in the foregoing pages. I have omitted the tail because, while there are a sufficient number of caudal vertebrae preserved to show conclusively that it was long and slender, there are not enough preserved in connection to determine its length. I have little doubt that the number of vertebrae exceeded sixty. The precise lengths of the digits are also in a measure conjectural, since in no specimen is a digit preserved complete. Sufficient phalanges, however, have been recovered to enable one to reconstruct the fingers and toes with little chance of error, following the arrangement determined in other contemporary reptiles. The first digit of the hand is purely conjectural. It must have been

small, and may have been absent; the hand upon the whole seems to have been much like that of *Varanosaurus brevirostris*. The lengths of the anterior ribs are determined from one specimen in which they are preserved nearly completely in relation with the vertebrae. The lengths of the posterior ribs are conjectural. It is also assumed that there are not more than seven cervical vertebrae; there is a strong possibility, however, that the neck was longer.

In the life restoration (Fig. 8) I have added the tail in like proportion to that of slender living lizards. That it was as long as the head, neck, and trunk together there can be scarcely a doubt, for it is not often shorter in swift-crawling reptiles; it may have been longer. In much probability the living animal was covered with corneous scales; one can hardly conceive of a reptile with habits such as *Araeoscelis* must have had as having a bare skin, and it is quite certain that the body was not protected with bony scutes.

HABITS

Just what is the significance of some of the peculiar characters possessed by *Araeoscelis* I am at a loss to conjecture. That the creature was a swift-moving, crawling reptile there can be no doubt. That it was arboricolous I also believe; the pointed and curved ungual phalanges determine the presence of sharp claws in the living animal. The unusual development of the calcaneum and outer toes seems to indicate springing habits, and the curved femora and elongated epipodials resemble those of *Scleromochlus*, of whose leaping powers

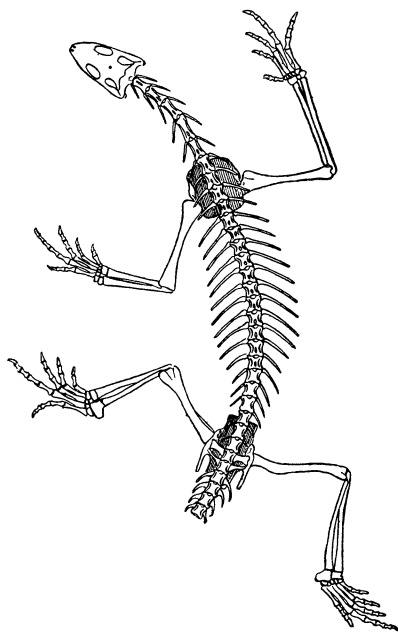


FIG. 7.—*Araeoscelis gracilis* Williston:
Restoration of skeleton, about one-fourth
natural size.

there can be little doubt. The extremely hollow bones also suggest arboricolous habits. Why the creature had such elongated cervicals I do not see. At one time the idea was entertained that *Araeoscelis* possessed more or less of a *Flughaut*, because of the development of the outer fingers and the possible loss of

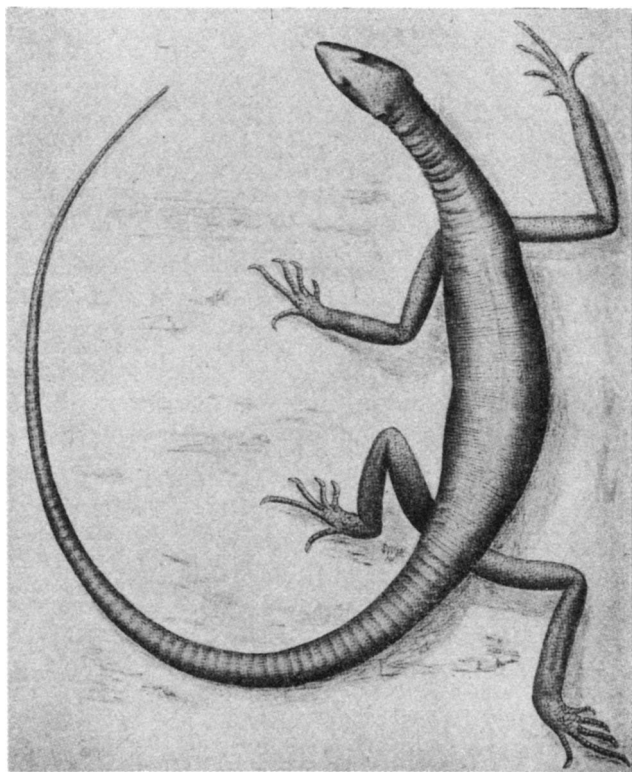


FIG. 8.—*Araeoscelis gracilis* Williston: Life restoration, about one-fourth natural size.

the first. And the cervical vertebrae certainly suggest those of the pterodactyls or birds, as Seeley has suggested of *Protorosaurus*. The presence of similar cervical vertebrae and hollow bones suggests somewhat similar habits for both these reptiles, but the vertebrae of *Protorosaurus* are clearly more like those of the crawling lizards, while those of *Araeoscelis* resemble more those

of snakes. The hind legs of *Protorosaurus* are longer than the front ones, and this is the case also with *Araeoscelis*, though not to the same extent. One can say with assurance that *Araeoscelis* was an extremely light and slender, terrestrial and arboreal reptile, with springing powers, and possibly with a parachute development of the body membrane. Its length, when adult, was about 2 feet.

THE SKULL OF *CASEA*¹

A preliminary description of the skull of *Casea*, as based on a single, not quite complete, specimen, has been given by me in my *American Permian Vertebrates*, with a promise of a further discussion whenever the additional material of the University collections should be worked out. One other skull has, so far, been discovered and prepared, though there is still a probability of others turning up in the future. This skull, unfortunately, had been somewhat injured in the collection of the material by the loss of much of the upper part in front of the parietal foramen. The right orbit is nearly complete and the lower part of the left, as also the lower part of the nares. The quadrates are somewhat displaced, but otherwise the skull is more perfect than the one previously described. The specimen is a part of a nearly complete skeleton which has not yet been worked out of its nodular matrix; it is of precisely the same size as the skeleton previously described. The premaxillae are complete, or nearly complete, and are in position with respect to each other and the maxillae. They project farther forward than did the incomplete ones of the previous specimen, terminating above in slender processes, which separate the nares narrowly. In the first-described specimen the nares had been somewhat injured, with the roof depressed, especially on the right side. The present specimen gives the lower side complete and quite undistorted, enabling me to restore the orifice with the aid of the other specimen, accurately, I think. It is possible that the orifice may have been a little higher than I have figured it (Figs. 9, 10). The nares, it is seen, are of enormous size, communicating immediately with the very large internal openings below

¹ Williston, *Jour. Geol.*, XVIII (1910); *American Permian Vertebrates* (1911).

them. Lying just within the orifice there is a thin, plate-like bone, evidently forming a turbinated structure, the sphenomaxillary.

Not much can be added to my description of the temporal vacuity. On the right side the orbital bar and inferior arcade are nearly complete, but on the left side they have been injured by the displacement of the quadrate. I think, however, as I suspected, that the vacuity is a little smaller than I figured it.

Nothing definite can be said as to the presence of a distinct quadratojugal bone.

The palate, fortunately, is in such preservation that its structure, save in details, is very clear. The whole surface is closed, as in *Pantylus*, and is covered with small, but pointed, conical teeth. Large orifices in front, corresponding with those shown in the former figure, are the nares, situated immediately below the external openings. The two sides of the palate show divisions so alike that one cannot resist the conviction that some of them,

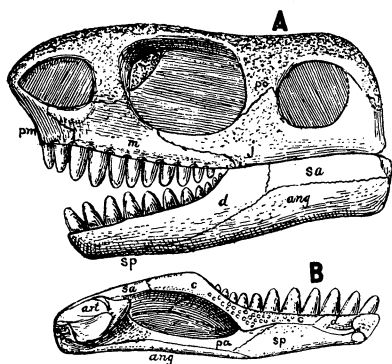


FIG. 9.—*Casea broilii* Williston: A, skull from the side; B, left mandible of same, from inner side, three-fifths natural size; *pm*, premaxilla; *m*, maxilla; *po*, postorbital; *i*, jugal; *d*, dentary; *sa*, surangular; *ang*, angular; *sp*, splenial; *art*, articular; *pa*, prearticular; *c*, coronoid.

at least, are sutural separations. Especially do the divisions running backward from the nares, which are not only alike on the two sides, but which agree with those of the former skull, indicate the sutures between palatines and pterygoids. One cannot be sure of the division between the pterygoids and vomers, covered, as the surface is, with numerous small teeth, which cannot be entirely freed from the matrix; but a symmetrical depression on the two sides seems to indicate the sutures, as shown by dotted lines in the figure. On either side behind, there are two divisions, which seem to be exactly alike on the two sides, one running forward and outward from the inner extremity of what would be the transverse bones if present; the other forward and inward to near the front end

of the interpterygoidal space. That all of these should be fractures, so exactly alike on the two sides, seems strange, but there can hardly be any other interpretation of the inner divisions, at least. They all bear teeth forming a continuous dentigerous surface between the mandibles, back of the nares. The two inner pieces are crowded nearly in contact over what is probably a slender parasphenoid in this specimen; in the other specimen, however, the base of a narrow parasphenoid is seen between the two sides.

In one or the other of the two skulls the structure of the posterior palatine region is definitely shown. The basisphenoid is a broad, flat, or gently concave bone, lying contiguous with the posterior processes of the pterygoids in front, and terminating in front, as I have figured it, apparently in a slender parasphenoid. Posteriorly the very stout stapes fits closely into an interval between the posterior angle of the basisphenoid and the exoccipitals. It is directed outward and backward, as a heavy, somewhat curved, cylindrical rod, to near the lower end of the quadrate, lying in close relation to the posterior process of the pterygoid.

The basioccipital forms the whole of the gently curved, cordate-shaped condyle, with a short, broad surface below in front. On either side the exoccipital is distinctly separated from the basioccipital, extending up on either side of the foramen magnum to near the top, as in *Dimetrodon*. These sutures are clearly shown; that between the exoccipital and paroccipital is less certain, though, from the agreement of lines on both sides in both specimens, I believe that the suture is situated as I have figured it in dotted lines. A small foramen for the posterior cranial nerves is visible as I

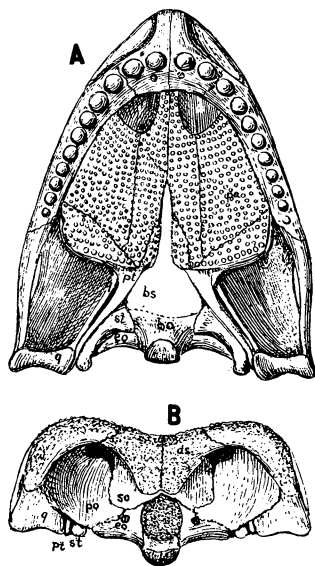


FIG. 10.—*Casea broilii*: A, skull from below; B, the same, from behind, three-fifths natural size; *po*, paroccipital; *pa*, palatine; *bs*, basisphenoid; *bo*, basioccipital; *pt*, pterygoid; *q*, quadrate; *st*, stapes; *eo*, exoccipital; *so*, supraoccipital; *ds*, dermosupraoccipital.

have figured it. The broad, outer concave surface of the occiput is formed chiefly by the paroccipital—I can detect nothing of the petrosal—leaving a small post-temporal vacuity above as an emargination of the upper side of the bone. At what seems evidently the junction of the paroccipital and supraoccipital there is a distinct notch, from which what seems to be a sutural line passes downward to join the exoccipital suture. The supraoccipitals form together a plate, somewhat convex in the middle above the foramen magnum, which extends upward to the under side of the parietals, as in lizards, but are covered, for the most part, by the loosely applied bones of the cranial roof, which descend to, or nearly to, the upper margin of the foramen magnum, with a slight notch in the middle. In one specimen they come quite to the margin, in the other they terminate some little distance above, owing to the greater depression of the skull roof in the former. These bones are rugose on the upper surface, forming a continuation of the cranial table. I suppose that they are the dermosupraoccipitals, joining the true supraoccipitals quite as in the cotylosaur *Labidosaurus*; but no certain line of distinction can be seen above. On the sides in each specimen a sutural line seems distinct, separating the bones from the lateral element, whatever it may be, of the suspensorial arch. As these lines agree in the two specimens, there would seem to be little doubt of their sutural character.

I cannot be sure of the structure of the process that curves downward on either side behind to cover the upper end of the quadrate. Since they join broadly the outer end of the paroccipitals behind, one would expect to find a distinct tabulare here; but if so, it cannot be demonstrated from these specimens.

With the exception of the loosely applied dermosupraoccipitals it will be seen that the whole structure of the occipital region, as I interpret it, resembles that of *Varanus*, except that the post-temporal vacuity is smaller, and that the exoccipitals take no part in the formation of the occipital condyle.

The sutures of the mandible are shown very satisfactorily in the two specimens, and doubtless I should have detected them in my previous study of them, had I then known what to expect.

The coronoid reaches posteriorly on the upper side of the meckelian orifice nearly to the anterior extremity of the articular; anteriorly this bone borders the alveolar margin as far forward as the third tooth. It is covered, for the most part, with small, conical teeth, like those of the opposite palatal surface. These teeth had been smoothly removed with the investing matrix in the first specimen described, but their attachments are clearly visible under a hand-lens; they are visible in the investing matrix of the second skull. The splenial enters into the mandibular symphysis below, as usual among the early vertebrates. The boundaries of the pre-articular are less distinct posteriorly, though certain evidences of sutural lines are visible as I have figured them.

The teeth in the second specimen are somewhat better preserved than in the first; they are of somewhat larger size, but their number and characters are quite the same.

Any comparison of the skull of *Casea* with that of other reptiles will be more or less speculative. It shares with *Diadectes*, *Pantylus*, and *Edaphosaurus* the short, broad skull and more or less elevated narial region. In all these the palatal region is practically closed in front and covered with more or less thickly set teeth, indicating similar food habits. From the nature of the obtuse mandibular and maxillary teeth, I had inferred herbivorous habits; but it is quite possible that the food may have consisted chiefly of the softer invertebrates. Against this assumption, however, is the very large abdominal capacity that suggests plant food. The skull, as I have before suggested, has a strange resemblance to that of *Amblyrhynchus*, the subaquatic Galapagos lizard, in the great development of the narial region.

The single large temporal vacuity reminds one of *Edaphosaurus*, but the intimate resemblances end there. Nor is there a very intimate relationship between *Casea*, the poliosaurids, as represented by *Varanoops*, or the ophiacodontids as represented by *Theropleura* or *Ophiacodon*. That the genus represents a distinct family there can be no doubt; its higher relationships must await further discoveries—I have little faith in phylogenetic speculations based on our present ignorance of the early reptilian faunas.

ARRIBASAURUS, A NEW GENUS OF THEROMORPH REPTILES
FROM NEW MEXICO

Among the collections made by Mr. David Baldwin for Professor Marsh more than thirty years ago, there is a considerable quantity of more or less broken and fragmentary bones of a small reptile from El Cobre Cañon, New Mexico. All of this material, or at least the greater part of it, was evidently collected from the surface at one spot where it had been washed from some bone-bed. The material consists, apparently, of the remains of a single species, represented by the bones of adults and young. Among the collections made by the University of Chicago expedition to the same region in the summer of 1911, there are a number of bones and fragments of bones collected from the surface near the west part of the same cañon, that evidently are of the same species as some if not all the remains of the Yale collection, if not also of the American Museum collection made by Baldwin for Professor Cope from El Cobre, which includes the type of the species *Dimetrodon navajoicus* Case. I should feel quite confident that the Chicago collection came from the same bone-bed deposit as the remains preserved at Yale University, were it not that the bones all seem to belong to a single individual, save for a small femur of a yet unnamed cotylosaur of very small size. Of the Yale material the larger part consists of the remains of immature animals, as shown by their smaller size and incomplete ossification of the ends of the long bones. There are, however, portions of the skeletons of at least two adults among the collection. The lower end of one of these adult specimens agrees so well with the humerus figured and described by Case under the name *Dimetrodon navajoicus*, that I feel fairly confident of their specific identity, notwithstanding the apparent absence of an ectepicondylar process in the specimen as figured by Case. That all this material at Yale and at Chicago belongs in a single genus there can be no reasonable doubt. If the adult specimens are later shown to belong to a distinct species it will be time enough to give a new name when the facts are known. The genus may therefore be defined as follows:

Arribasaurus, genus new. Teeth slender, conical, more elongate anteriorly, short and closely placed posteriorly. Spines of verte-

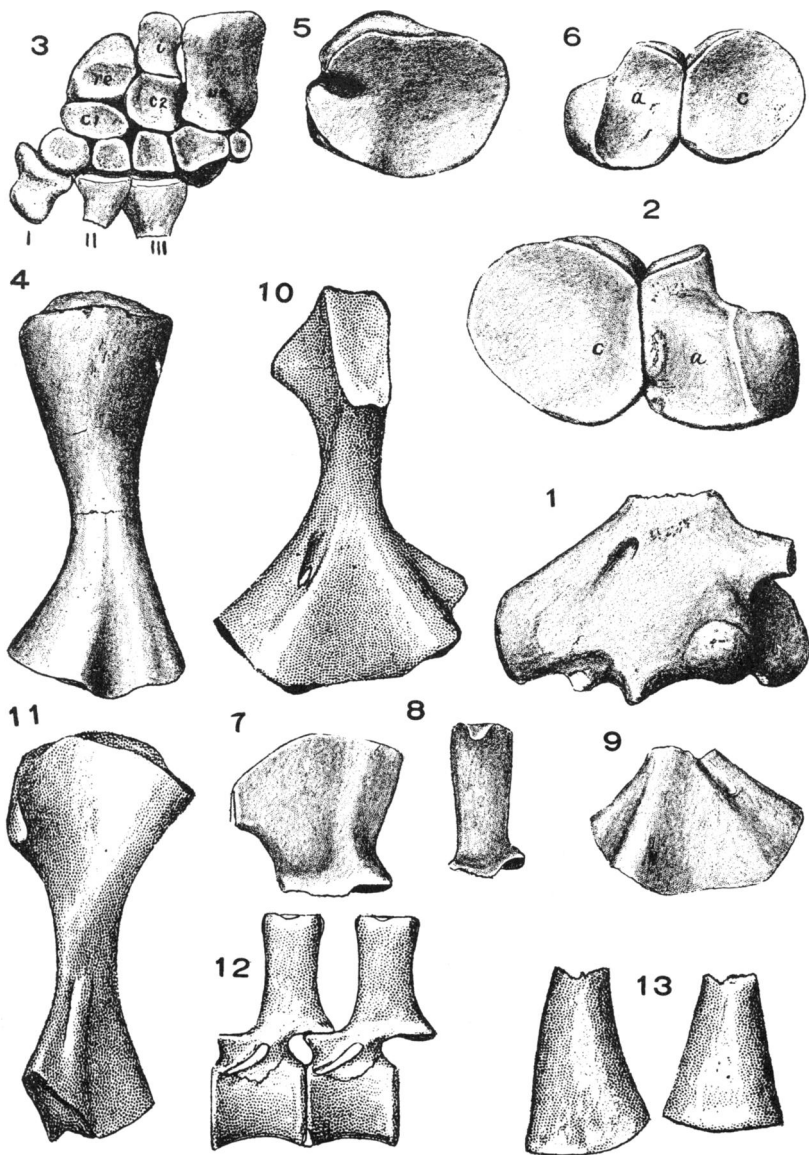


FIG. 11.—*Arribasaurus navajoicus* Case: 1, distal end of left humerus, ventral side; 2, calcaneum and astragalus, from the front; 3, left carpus, from the front; 4, left femur, dorsal side; 5, pubis; 6, right calcaneum and astragalus of young, from the front; 7, spine of axis; 8, spine of dorsal vertebra; 9, distal end of young humerus; 10, right immature humerus, dorsal side; 11, the same, ulnar side; 12, two dorsal vertebrae, from the side; 13, distal end of tibia; 14, distal end of fibula. All natural size.

brae (Fig. 11, 8, 12) short and flattened, with the upper extremity flattened ovate in section; axis with a broad spine, as in the Poliosauridae; diapophyses with a continuous articular surface, directed downward and forward, showing holocephalous ribs, as in *Ophiacodon*. Humerus (Fig. 11, 1, 10, 11) with the lateral process high up on the shaft; distal extremity much expanded, its plane nearly at a right angle with that of the proximal end; carpus (Fig. 11, 3) very much as in *Ophiacodon*; the first centrale and inner carpalia larger. Pubis (Fig. 11, 5) subcircular or subquadrate in outline, with the obturator foramen more or less notched (in the young at least); ischium and proximal tarsal bones (Fig. 11, 2, 6) as in *Ophiacodon*; femur with a rather slender shaft (Fig. 11, 4). Length of animal probably about 5 feet.

So far as the skeletal bones and teeth are concerned, the genus seems to be related to *Ophiacodon*, but the pubis shows very distinctive characters, and the spines of the vertebrae are relatively much shorter; the humerus is also much more elongated. On the strength of the pubis alone, a very characteristic bone in the Pelycosauria, the genus is, I think, eliminated from the Poliosauridae or Ophiacodontidae; and the teeth will exclude it from the Sphenacodontidae. The pubis has a distinct resemblance to one which I figured erroneously as a calcaneum in my *American Permian Vertebrates* (Plate XXXI, Fig. 10, and Plate XXXII, Fig. 11), from the Craddock bone-bed, Texas; and it is possible that the femur, also figured in this work on Plate XXX, Fig. 4, may belong with this pubis, a yet unnamed genus, that may prove to be related to the present one.

THE PRIMITIVE STRUCTURE OF THE MANDIBLE IN REPTILES AND AMPHIBIANS

Until within recent years the mandible of reptiles was thought to be composed of not more than six bones, originally named by Cuvier and Owen the articular, angular, surangular, coronoid, splenial, and dentary. In *Sphenodon* only was it known that one of these bones, the splenial, was absent. The bone long known as the splenial in the turtles occupies an anomalous position for that bone, overlying the inner side of the articular and remote

from the position of the splenial in other reptiles. Baur,¹ in 1895, discovered in the extinct *Toxochelys* a bone that corresponds to the true splenial of other reptiles, and recognized for the first time that the so-called splenial of other turtles really is homologous with a dermal element which is either wholly wanting or is indistinguishably fused with the articular in all other reptiles then known. Unfortunately, assuming that the bone so called in the *Chelonia* was the true splenial, he changed the names of the elements in other reptiles to correspond, naming that originally called the splenial by Owen the presplenial, causing thereby much confusion in nomenclature. In 1903 I recognized² for the first time in another reptile this dermogenous element, in the plesiosaurs, and corrected Baur's error by naming it the prearticular, retaining the names of all the other elements as originally applied by Cuvier and Owen. Soon afterward Case recognized the prearticular in the Pelycosauria, and Branson in the Stegocephalia. Since then the name has come into general use, though other names were later proposed for the same bone (dermarticular Kingsley, goniale Gaupp). Five years ago I expressed the conviction that a separate prearticular would be found characteristic of all early reptiles; we now know that to be the fact. Typically the bone overlies the inner side of the articular, forming the inner margin of the supra-meckelian orifice, and the posterior and superior margin of the posterior inframeckelian foramen, when it is present, its anterior end intercalated between the splenial and the coronoid. In other words, it has precisely the same relations as has the anterior inner part of the angular in the crocodiles (Fig. 12), in which no evidence has so far been adduced of a prearticular ossification. One wonders whether embryological investigation may not show a fused condition of prearticular and angular in these reptiles; in which case the so-called angular would properly be called the angular-prearticular, just as the so-called articular of lizards is really the articular-prearticular.

In all later reptiles the coronoid is a small element occupying the eminence of the mandible back of the teeth, articulating with

¹ Baur, *Anat. Anzeiger* (1895), p. 412.

² Williston *Field Columb. Mus. Publ.*, No. 73, p. 30.

the dentary, surangular, and prearticular or angular, and also the splenial when present. It never extends farther forward than

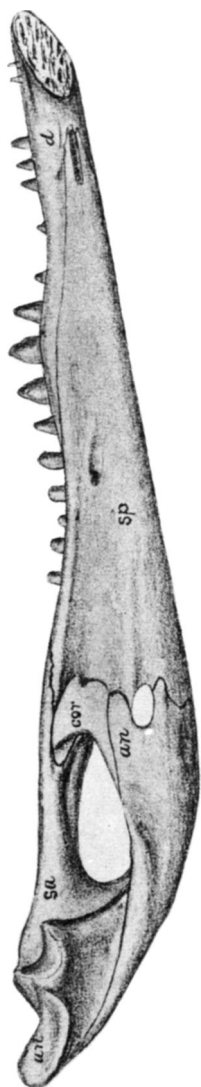


FIG. 12.—*Alligator mississippiensis*: Left mandible, inner side. Explanations as in Fig. 13.

the posterior part of the dental series. In the same plesiosaurian mandible in which I recognized a separate prearticular, there was "a long, slender, flattened, trihedral bone, extending far forward along the alveolar margin, meeting its mate in the median symphysis" (Fig. 16), which I was forced to call the coronoid, though it was utterly unlike anything that had previously been recognized as the coronoid. Only within recent years has this peculiar structure of the coronoid been recognized in other plesiosaurs, by Andrews and Linder; doubtless it is characteristic of the order, testifying to its primitive origin. This elongate form of the coronoid is now known to be characteristic of all primitive reptiles. In these reptiles it lies along the inner alveolar margin of the mandible, extending toward the symphysis, but entering into union with its mate only in those reptiles having a long mandibular symphysis. Its posterior end occupies the position of the coronoid of later reptiles, that is, articulating with the anterior superior part of the surangular, chiefly on the inner side of the mandible, and forming the anterior margin of the meckelian orifice. It articulates with the prearticular below; it is always narrow.

The splenial in all modern reptiles, when present, is a thin bone covering more or less the inner side of the mandible anteriorly and the meckelian groove, extending rarely as far forward as the symphysis; it is not visible on the outer side of the mandible, or, if so, only to a very slight extent. As I stated some years ago,¹ "in all or nearly all reptiles having a greatly elongated

¹ Williston, *Jour. Geol.*, XVI (1906), 6.

mandibular symphysis, the splenial takes part in its union." But, this symphyseal union of the splenials in such forms is doubtless due to the recession of the symphysis, rather than to the retention of a primitive character, since in the alligator and crocodile, with a short symphysis, the splenials do not meet, while in the gavial, with a long symphysis, they do.

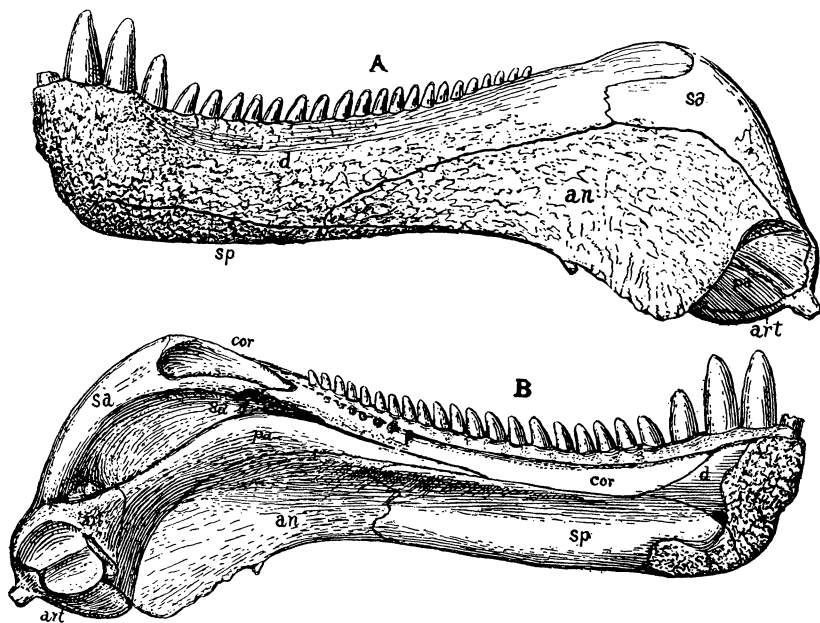


FIG. 13.—*Dimetrodon incisivus* Cope: A, left mandible, outer side; B, inner side of same; cor, coronoid; d, dentary; sa, surangular; an, angular; art, articular; pa, prearticular; sp, splenial.

Not only is the symphyseal union of the splenials a primitive character, as was first stated by me in 1911¹ and reaffirmed the following year, but, unlike modern reptiles, it enters more or less into the outer surface of the mandible, as I have figured it in various cotylosaurs (*Limnoscelis*, *Labidosaurus*, *Captorhinus*). These primitive characters may be summarized as follows:

The primitive mandible of reptiles is composed of seven distinct bones, the articular, prearticular, angular, surangular, coronoid, splenial, and dentary. The coronoid is elongated, extending along

¹ Williston, *American Permian Vertebrates*, p. 30.

the alveolar margin of the teeth toward the symphysis, and often bearing teeth. The prearticular forms the inner border of the meckelian orifice and is intercalated between the coronoid and splenial anteriorly. The splenial takes part in the mandibular symphysis, and is more or less visible on the outer side of the

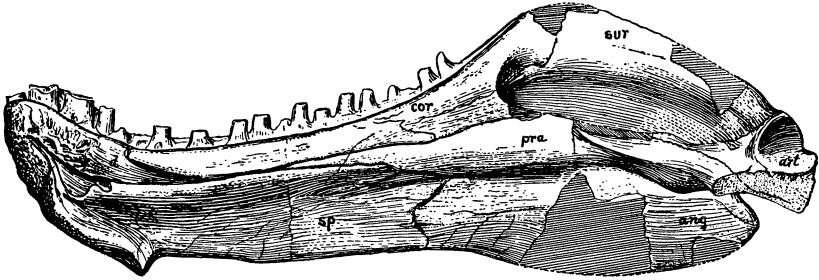


FIG. 14.—*Dimetrodon*, sp.: Right mandible, from inner side. Explanations as in Fig. 13.

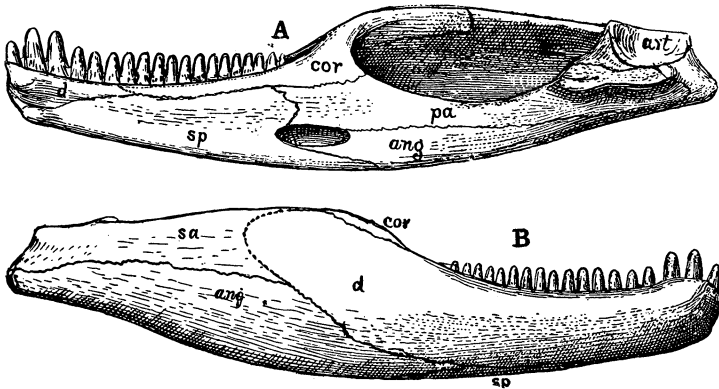


FIG. 15.—*Labidosaurus hamatus* Cope: A, right mandible, inner side; B, the same, outer side. Explanations as in Fig. 13.

mandible. A posterior inframeckelian foramen is present in the most primitive reptiles.

These characters I have determined in six different genera of Permian reptiles, and I doubt not that they will be found in all, from the Lower Permian at least. Figures of the mandibles of four of these are given herewith, and do not need detailed description (*Dimetrodon*, Figs. 13, 14; *Casea*, Fig. 9; *Labidosaurus*,

Fig. 15; and *Captorhinus*, Fig. 16). Photographic copies of the mandible of *Dimetrodon*, precisely as here figured (Fig. 13), were distributed to some of my correspondents in August of 1913. I was not then confident of the continuity of the coronoid bone throughout, and so briefly described it in *Science* of October 10, 1913, as possibly, though not probably, composed of two bones, the anterior one of which I called the alveolar. Later material satisfied me that there is but a single bone. Dr. Broom¹ refers to this description as of a distinct alveolar bone; doubtless it was an oversight, since he received a copy of Fig. 13 in August, as also my figures of the mandibles of *Trimerorhachis* and *Labidosaurus*, before he wrote his paper.

Since the foregoing went to the printer I have received from Dr. Broom another paper, published February 24, 1914, containing a description and figure of a mandible of a pelycosaur

preserved in the National Museum, which he doubtfully referred to either *Dimetrodon* or "*Naosaurus*" (*Edaphosaurus*)! The only addition this paper makes to our knowledge is the precise connection between the coronoid and prearticular. He determines, however, without hesitation or doubt a suture separating the coronoid into two bones, the anterior of which he calls the precoronoid. At my request, Mr. Gilmore kindly sent me the specimen upon which Broom's studies were based. It is very clearly a species of *Dimetrodon*. I give herewith a more accurate figure of the specimen (Fig. 14). All the sutures, aside from the one in question, are

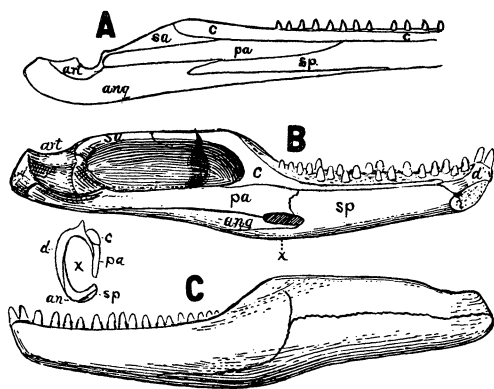


FIG. 16.—*Trinacromerum osborni* Williston: Left mandible to symphysis, inner side, after Williston, 1903; B, *Captorhinus aguti* Cope, left mandible, from within; C, the same, outer side. Explanations as in Fig. 13.

¹ Broom, *Bull. Amer. Mus. Nat. Hist.* (November, 1913).

clearly shown, especially in connection with my previous figure which Dr. Broom had at the time of his studies. That there is a real suture dividing the coronoid is not impossible, but there is nothing in the specimen to prove that it is not a crack, and not until it is corroborated by additional material should his figure be accepted as certain. Dr. Broom has made mistakes before in his hasty identification of cracks as sutures, and this may be another one. Dr. Broom states that he has "recently" seen a copy of my figure of the *Dimetrodon* jaw as here given (Fig. 13). "Recently" is evidently here used in a relative sense, since he

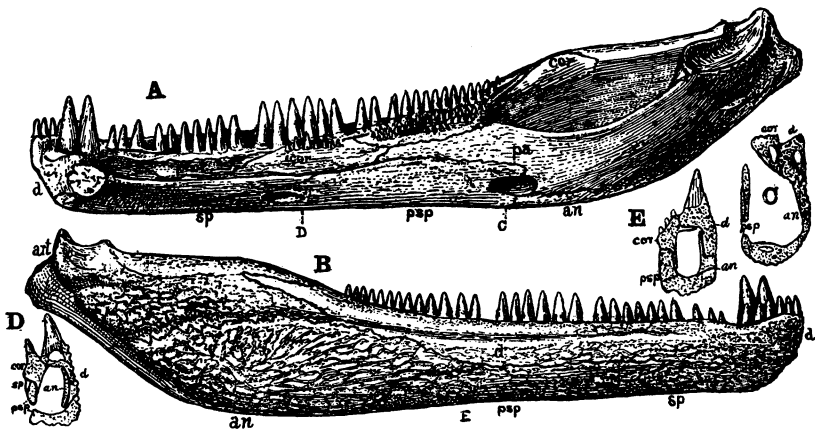


FIG. 17.—*Trimerorhachis alleni* Case: A, right mandible, inner side; B, the same, outer side; C, D, E, sections of mandible as designated; *psp*, postsplenial; *cor*, coronoid; *icor*, intercoronoid; *pcor*, precoronoid. Other explanations as in Fig. 13.

first saw the figure before he began his study of the American mandibles, in August, more than three months before he studied the specimen in the National Museum.

AMPHIBIANS

In the structure of the mandible the amphibians are remarkably intermediate between the early reptiles and the contemporary crossopterygian fishes, differing from the latter chiefly in the reduced number of coronoids, and from the former chiefly in the possession of two additional coronoids and a splenial.

Until very recently our knowledge of the stegocephalian mandibular structure has been imperfect and more or less erroneous. Branson for the first time recognized in an amphibian the presence of a distinct prearticular, and correctly homologized what is now

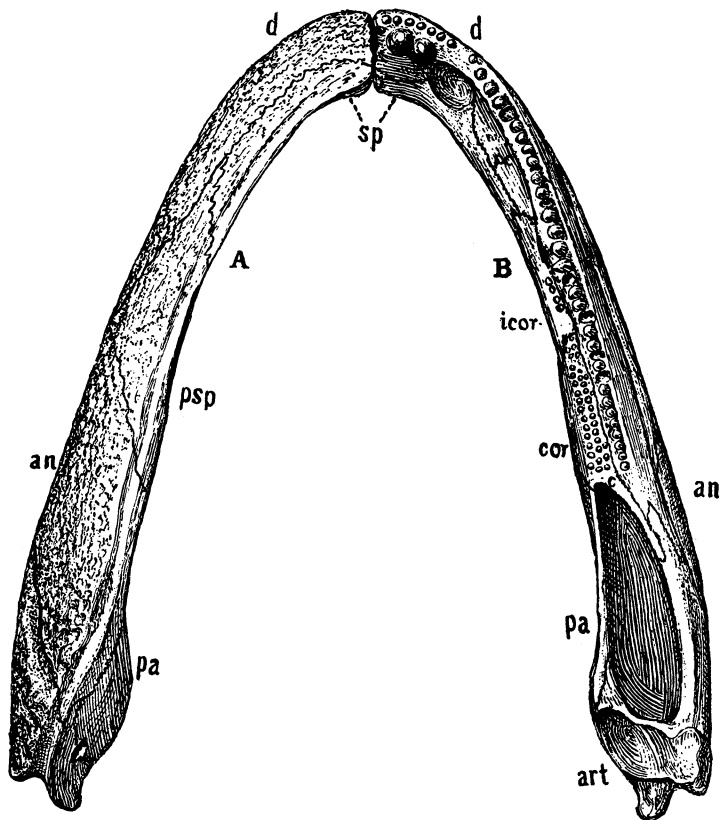


FIG. 18.—*Trimerorhachis insignis*; A, right mandible, from below; B, the same, from above. Explanations as in Figs. 13 and 17.

known as the true splenial with the infradentary of fishes. He erred in uniting the postsplenial with the angular, and in calling the intercoronoid and precoronoid the splenial. He also identified the true coronoid correctly. Watson very recently correctly homologized the true splenial with the infradentary of Branson,

and correctly identified the anterior coronoid. He erred in distinguishing the limits of the prearticular and in giving to the true coronoid the name epicoronoid as an element peculiar to amphibians.

The posterior splenial (Fig. 17, *psp*) was, I believe, for the first time recognized in any amphibian by me in the early part of last August, and its discovery communicated to several correspondents, as was also the structure throughout of the mandible of *Trimerorhachis*, with the exception of the sutures separating the anterior coronoids. Photographic copies of the figures of the mandible of this genus, as published by me in a preliminary paper in the October-November (1913) number of the *Journal of Geology*,

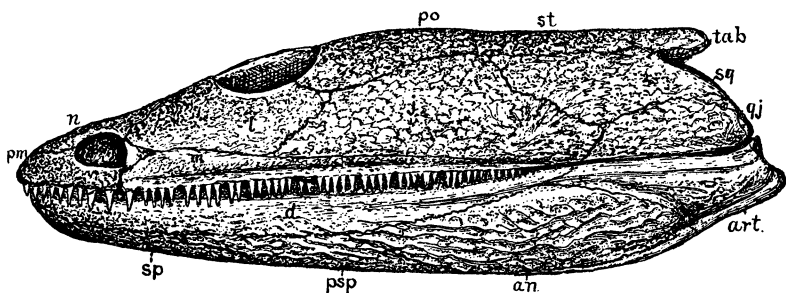


FIG. 19.—*Trimerorhachis insignis* Cope: Skull, from the side, one-half natural size. Explanations as in previous illustrations.

were distributed to various correspondents in September and October. That figure differs from the ones here shown only in the less precise sutural line between the coronoid and prearticular, and in the absence of the sutures between the anterior coronoids. All these corrections were definitely and positively recognized by me in a later collection of material sent me by Mr. Lawrence Baker in October a short time before the publication of the paper by Dr. Broom. From this it results that I had discovered the postsplenial and had suggested that name for it before Dr. Broom began his studies of the mandible; and that Dr. Broom discovered the two anterior coronoid elements before I did. The names then, postsplenial, intercoronoid, and precoronoid, may properly be retained for the new elements, provided that nowhere

in the ichthyological literature there are prior names for these elements in the crossopterygian fishes.

Although there has been an unnecessary duplication of studies which might have been avoided, the results are fortunate in their independent corroboration, placing at rest any doubts as to the real structure of the stegocephalian mandible. Dr. Broom's figures are inaccurate in detail, as will be seen by comparing them with those herewith given.

A detailed description of the elements is unnecessary; the illustrations will explain them better. In none of the many specimens have the sutures between articular and surangular been distinguished. I have spent much time in making sections of the articular end and in corroding with acid many specimens, but wholly in vain. There are certain variations in different specimens which it may be well to notice. The posterior inframeckelian foramen is sometimes situated farther in advance, and is almost wholly bordered above and below by the postsplenial. The splenial usually enters very distinctly into the mandibular symphysis; in some specimens it takes only a slight part. A structure like that of *Trimerorhachis* I have observed in *Eryops*, *Diplocaulus*, and other stegocephalians. I also find the postsplenial in *Anaschisma*, but have not distinguished the anterior coronoids.

SUMMARY

The mandible of the primitive amphibians differs chiefly from that of the early reptiles in the division of the coronoid into three elements, or possibly four, and in the division of the splenial into two. The surangular cannot be distinguished, if present.